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POPULATION ECOLOGY OF THE LITTLE BROWN BAT, *MYOTIS LUCIFUGUS*, IN INDIANA AND NORTH-CENTRAL KENTUCKY

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POPULATION ECOLOGY OF THE LITTLE BROWN BAT, *MYOTIS LUCIFUGUS*, IN INDIANA AND NORTH-CENTRAL KENTUCKY

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FOREWORD

THE secretive behavior and nocturnal activity of bats makes them difficult to observe. Casual observation is limited to hibernating bats, to the occasional bat flitting after insects at twilight, or to an uninformative squeak or odor emanating from a daytime roost. The development of marking techniques and the establishment of a Federal Bat-Banding Office to issue bands and process recapture data made it possible to identify and follow individual bats over long distances and time spans. Bat banding projects combined with regular recapture programs have produced great amounts of ecological data.

When the second author began teaching mammalogy in 1950, relatively little was known about the natural history of bats. The present study was begun to provide to students and the public some new information on biology of bats in the eastern United States.

Many people contributed to this research. Regular gathering of quantities of data was possible only with the continuing interest of numerous Earlham College students. Notable among these were W. Wilson Baker, William H. Buskirk, Edward B. Churchwell, Anthony F. DeBlase, Bernard Gross, Donald R. Hendricks, Stephen Hinshaw, Pamela P. Humphrey, Keith C. Koontz, Richard S. Mills, George V. Powell, Jay H. Schnell, Frank S. Sterrett, and Nixon A. Wilson. Gertrude L. Ward participated in the field work, handled project correspondence, and maintained accurate records of the data. Personnel of the Bat-Banding Office, Bird and Mammal Laboratories, National Museum of Natural History, Washington, D. C., who greatly facilitated this study include Emma Charters, Edward L. Davis, Arthur M. Greenhall, Barbara Harvey, Clyde Jones, and John L. Paradiso. Wayne H. Davis and Russell E. Mumford reported many recaptured bats. Many friendly landowners in Indiana and Kentucky, especially Ella Wright, Carl Palmer, and the late Roy Randel, cooperated by permitting us to work on their property. Useful unpublished data were provided by Bryan P. Glass, Edward Hinckley, Thomas H. Kunz, James C. Lewis, William E. Mahan, Richard S. Mills, and Merlin D. Tuttle. Bryan P. Glass, John A. Morrison, Robert D. Morrison, and

Jerry L. Wilhm criticized an early draft of the manuscript, which was submitted by the first author to Oklahoma State University in partial fulfillment of requirements for the degree of Doctor of Philosophy. We gratefully acknowledge the valuable editorial assistance of James N. Layne. This work was supported by grants from the National Science Foundation (nos. 9321, GE4070, GE6193, and G2-2807) to Earlham College and by the Joseph Moore Museum.

CONTENTS

Introduction 1

Methods 1

Population Types and Habitat 3
- Nursery Populations 3
- Shelters or Summer Male Roosts 5
- Winter Populations 6

Movement Patterns 7

Population Size and Fluctuations 18
- Nursery Populations 18
- Swarming Groups 22
- Winter Populations 24

Sex Ratios 27
- Nursery Populations 27
- Shelter Groups 30
- Swarming Groups 32
- Winter Populations 33

Reproduction and Development 38
- Age at Sexual Maturity 38
- Breeding Season 38
- Parturition 39
- Period of Maternal Care 40
- Litter Size and Number of Litters Per Year 40
- Proportion of Breeding Females 41

Survival and Mortality 43
- Survival 43
- Natural Causes of Mortality 53
- Human-Related Population Declines 55

Ecological Strategies 61

Summary 71

Literature Cited 75

Index 80

INTRODUCTION

The little brown bat, *Myotis lucifugus,* is one of the most abundant and widely distributed insectivorous bats in the United States and Canada. Although this species has been the subject of many life history studies (reviewed by Barbour and Davis, 1969), its population ecology is poorly known. The purpose of the present study was to ascertain the ecological characteristics of the several types of populations formed by *M. lucifugus* and to determine how such populations interact.

METHODS

Populations were located by an extensive publicity campaign involving newspaper articles, distribution of posters, radio announcements, and contacts with game wardens, state park superintendents, county extension agents, exterminators, and spelunkers. Size was estimated and samples were taken at 23 summer populations and eight winter populations. Phenological patterns, changes in age and sex structure, and reproductive events were documented with 408 population samples and 135 flight counts. Bats in buildings and caves were captured by hand or with long-handled nets or bottle forceps. In spring and autumn, bats were captured by placing mist nets across cave entrances at night. Captured animals were banded and released. Bats were classified as immatures or adults according to the condition of phalangeal epiphyses. A total of 71,706 *M. lucifugus* was banded from 1952 to 1969. Of this number, 10,760 individuals were recaptured a total of 14,336 times.

The seasons of the year are delimited in this report to include specific events of the annual cycle of *M. lucifugus,* as follows. Winter, 16 October to 31 March, is the period of hibernation. Spring, 1 April to 31 May, includes spring movements and most of the gestation period. Summer, 1 June to 25 July, includes parturition, maternal care, and the first few days of flight of the

young. Autumn, 26 July to 15 October, includes dispersal from the summer roosts, autumn migration, and autumn swarming behavior. Although some yearly phenomena extend over two or three seasons and some dates vary latitudinally, the above definitions provide a useful framework for discussion.

Most bats were recaptured at the banding site. Recaptures at new sites are designated "foreign" recaptures. Foreign recaptures made by persons other than bat biologists are not restricted to the roosts familiar to us and are free of our geographic sampling bias. These are distinguished as "citizen" recaptures.

All data reported and cited refer to the eastern subspecies, *M. l. lucifugus,* unless otherwise indicated.

POPULATION TYPES AND HABITAT

Nursery Populations

During the warm months female and a few male *M. lucifugus* congregate in nursery colonies where the females bear and rear their young. Fifty nurseries were found in Indiana. Cope *et al.* (1961) published a map of the 38 nurseries found by the end of 1960. Periodic samples were taken at 23 nurseries (Fig. 1) that were accessible for study and had large populations.

Most nursery roosts were in attics of houses and churches, and a few were in barns or school buildings. Most populations occupied single buildings, but several large groups (Thorntown, Franklin, Brookville, Tunnelton, Shoals) used from two to four buildings, such as a house and nearby barn or several houses in a small town. Movement records show that such a group behaved as a single population. One group was found in an elm tree (*Ulmus americana*) near Williamsburg, Wayne Co., Indiana, on 22 May 1967. Approximately 15 bats flew from under loose bark when the tree was pushed over with a bulldozer. Three captured individuals were adult female *M. lucifugus*. This site could have been a spring transient roost rather than a nursery. Although *M. lucifugus* in the wild is thought to locate nurseries in trees and rock crevices, no such roosts have been reported previously. The only other reports of nurseries not in buildings are two populations in caves in Illinois (Myers, 1964) and one (*M. l. carissima*) in an Oregon Cave (Bailey, 1936).

Most roosts were hot, dark, poorly ventilated, and contained several small access holes in the roof, eaves, or walls. The species sometimes occurred in the well-lighted and ventilated attics or open barns commonly inhabited by the big brown bat, *Eptesicus fuscus*. High nursery temperature may be a key factor in the energetic economy of reproduction and growth. Davis (1967*b*) suggested that this species may require high nursery temperatures, which promote rapid growth of the young. Studier and O'Farrell (1972) found that pregnant female *M. l. occultus* and young less than 10 days old were poor thermoregulators.

We commonly observed behavioral thermoregulation similar

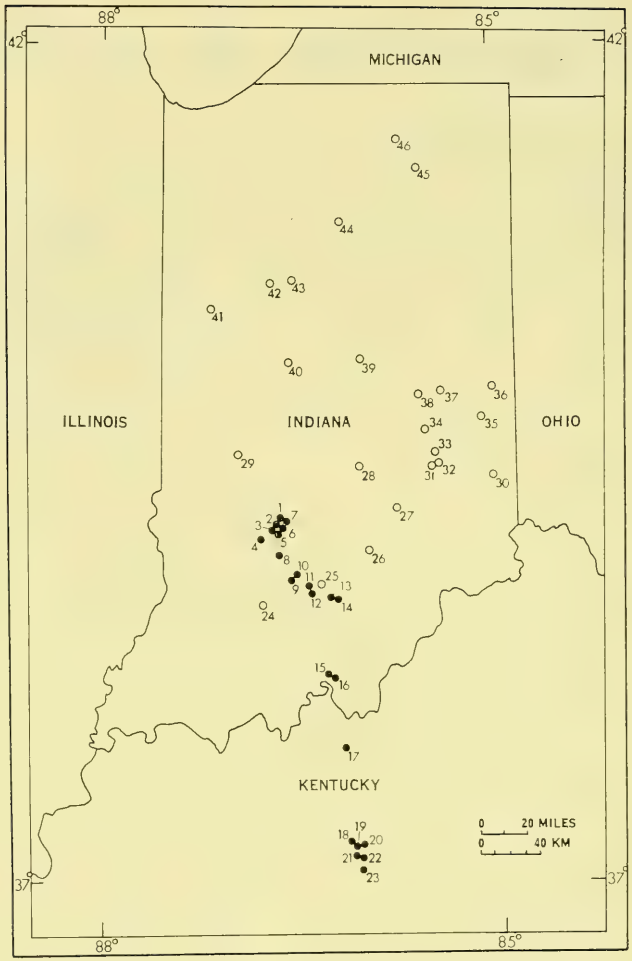

Fig. 1. Distribution of *Myotis lucifugus* populations mentioned in the text. Open circles are nursery populations in buildings; closed circles are winter populations in caves. Localities: 1, Grotto Cave; 2, Coon's Cave; 3, Brinegar's Cave; 4, Ray's Cave; 5, Buckner's Cave; 6, Shaft Cave; 7, Salamander Cave; 8, Sullivan's Cave; 9, Blue Spring Cave; 10, Donnehue's Cave; 11, Bronson's Cave; 12, Donaldson's Cave; 13, Endless Cave; 14, Nymon Cave; 15, Wyandotte Cave; 16, Parker's Pit; 17, Wind Cave; 18, Dixon Cave; 19, Mammoth Cave; 20, Colossal Cave; 21, Long's Cave; 22, Short Cave; 23, Coach-James Cave; 24, Shoals; 25, Tunnelton; 26, Cortland; 27, Newbern; 28, Franklin; 29, Reelsville; 30, Brookville; 31, Milroy-south; 32, Milroy-east; 33, Rushville; 34, Occident; 35, Pennville; 36, Williamsburg; 37, New Castle; 38, Shirley;

to that reported in the Yuma bat, *Myotis yumanensis*, by Licht and Leitner (1967) and suggested for *M. lucifugus* by Cagle and Cockrum (1943). On cool days we found the bats in the warmest unexposed refuges available, whereas on hot days most of the bats hung exposed to the attic air in loose clusters along the peak and on rafters and end walls below the peak. On extremely hot days most bats moved down the walls and rafters, many going as far as the space between the inner and outer walls of the building—below the level of the attic floor. The maximum vertical distance between roosting sites selected on cool and hot days varied from one to six meters, depending on the structure of the building. The sites chosen for roosting on a particular day had great influence on the proportion of the population we were able to capture.

Most nurseries were located within a few hundred meters of a pond, stream, or river, and the bats flew directly to the water when emerging in the evening. Similar observations were made by Davis and Hitchcock (1965).

Shelters or Summer Male Roosts

Several authors have made casual reference to individuals or small groups of *M. lucifugus* inhabiting rock crevices, tree hollows and loose bark, and small openings in buildings during the warm months (Griffin, 1940*b*; Smith, 1954; Cope *et al.*, 1961; Krutzsch, 1961; Fenton, 1969*b*). Specific locations of such shelters include house shutters (Sherman, 1929; Miller, 1955; Fenton, 1970), cottage flashing (Hitchcock, 1940; Fenton, 1970), clapboard siding of houses (Glass and Ward, 1959; this study), under rocks (Fenton, 1970), under a shale ledge (Baker, 1964), a stone quarry (Jones, 1964; Kunz, 1965), a copper mine (Stones and Oldenburg, 1968), and caves (Krutzsch, 1961; Davis and Hitchcock, 1965; Heltsley, 1965). Refugia in buildings found in this study were in barns or picnic pavilions of Turkey Run State Park, Parke County; Jackson County State Park; Shades

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39, Cicero; 40, Thorntown; 41, Pine Village; 42, Pittsburg; 43, Camden; 44, Macy; 45, Etna; 46, Benton.

State Park, Montgomery County; and Ferdinand State Park, Dubois County. No major cave shelters were found but intermittent use of Donnehue's, Ray's and Wyandotte caves was noted. Most bats found in these situations were males.

Some of these shelters were transient roosts, but others had a long history of regular use. Droppings indicated repeated occupancy of two building shelters (Hitchcock, 1940) and a cave (Krutzsch, 1961). Sherman (1929) observed *M. lucifugus* at a building shelter from 1915 to 1928. Miller (1955) reported use of a shelter from 1942 to 1954. Collections and sample data were taken for six years between 1954 and 1969 at another shelter (Glass and Ward, 1959; this study). On the basis of these records, it appears that substantial numbers of *M. lucifugus*, mostly males, roost in shelters in the warm months.

Winter Populations

M. lucifugus hibernates in caves and mines during the winter. Thirty-six caves in Indiana and 18 in Kentucky were surveyed for winter populations. The species occurred in 27 of the Indiana caves and six of the Kentucky caves. Six Indiana caves and two Kentucky caves were selected for repeated sampling (numbers 1, 2, 4, 10, 12, 15, 17, and 20 in Fig. 1) because of large population size.

The winter roost sites of *M. lucifugus* were relatively uniform and stable in microclimate, being cool and humid with almost no air flow. Although measurements of *M. lucifugus* hibernaculum microclimate are available (see Myers, 1964), apparently no one has examined winter roosts for seasonal variations in temperature, humidity, and air flow which might cause winter population changes.

MOVEMENT PATTERNS

Since extensive bat banding programs have begun in North America, *M. lucifugus* has become well known as a migratory species. Migratory movements of *M. lucifugus* have been recorded in the eastern United States and Canada by Griffin (1940*a*, 1945), Gifford and Griffin (1960), Davis and Hitchcock (1965), Hitchcock (1965), and Fenton (1970). Less extensive information on *M. lucifugus* migration is available for the midwestern United States, although several field projects are in progress. Humphrey and Cope (1964) reported winter recaptures of bats banded at a single nursery in Indiana. Davis *et al.* (1965) and Barbour and Davis (1969) presented migration data from nurseries and hibernacula in several areas of Kentucky. Myers (1964) documented migration from hibernacula in Missouri.

In the present study 895 (1.25 per cent) of the banded bats were recaptured away from the banding site. Movement analysis is based on 845 of these foreign recaptures, with repetitious captures at new locations excluded. Most autumn and spring records were of bats netted at cave entrances rather than captured at roosts. In no cases are the details of night-to-night movement known, and probably few of these movements are straight through space and regular through time as simple maps and tables imply.

Autumn migration occurred from the last week of July to mid-October. Figures 2–7 illustrate autumnal migration patterns. The net distance of autumn migration ranged from 10 (Fig. 6) to 455 kilometers (Fig. 2) with an average distance of 100 kilometers. Most migration was from north to south but some movements occurred in all directions, depending on nursery location. Wintering areas used by bats from each nursery were partially distinct. Migratory movements may take as few as two days. Possibly sampling designed to measure minimum movement time would show rapid movements to be typical.

Autumn migration often differed from a simple linear pattern. Other types of movement that occurred during the migration period included dispersal or wandering, transient visitation to

Fig. 2. Foreign recaptures in any winter of female *M. lucifugus* banded at the Etna nursery (open circle) in summer. Numbers indicate more than one such movement.

non-home nurseries, swarming at caves, secondary dispersal, and secondary migration.

Autumn dispersal and transient nursery visitation may be identical but differed in the way we detected them. Dispersal was exhibited by 61 *M. lucifugus* banded at nurseries in summer

FIG. 3. Foreign recaptures in any winter of both sexes of *M. lucifugus* banded at the Thorntown nursery (open circle) in autumn.

or autumn and reported as citizen recaptures; whether the recapture sites were nursery roosts is unknown. A relatively large number (17) of these movements occurred in autumn or from summer to autumn. The individuals involved included one adult female, two immature females, four immature males, and four females and six males of unknown age. No directional pattern was apparent in dispersal movements. We recorded transient nursery visitation in autumn nursery population samples. Such movements showed no strong directional pattern or age or sex trends, took as few as two days, and ranged from 71 to 134 kilometers. Some of these movements may have followed secondary dispersal (see below) and thus have been indirect.

Autumn swarming is a phenomenon in which large numbers of bats of several species fly in and out of cave entrances from dusk to dawn. Similar but less intense activity also occurs in the spring. Information on movements associated with such swarm-

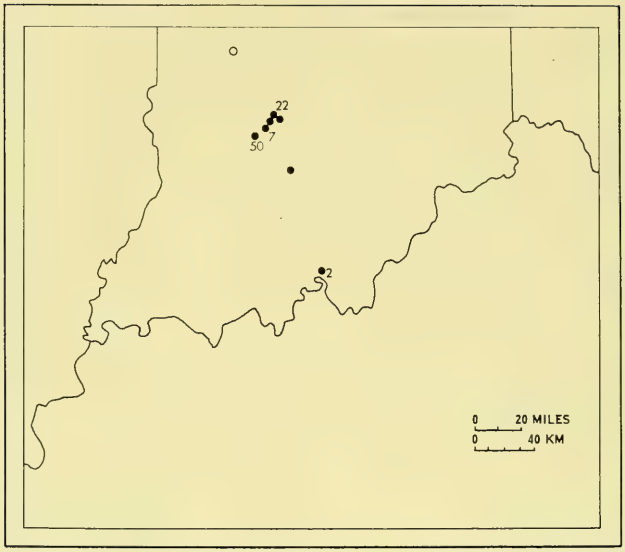

FIG. 4. Foreign recaptures in any winter of *M. lucifugus* of both sexes banded at the Reelsville nursery (open circle) in autumn.

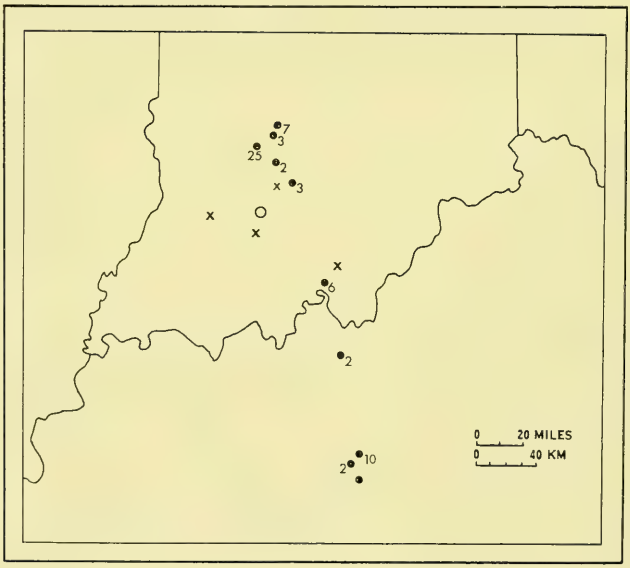

FIG. 5. Foreign recaptures in any winter of *M. lucifugus* of both sexes banded at the Shoals nursery (open circle) in autumn. "X" indicates a citizen recapture.

ing is based on netting at Wyandotte Cave from 1961 to 1965 (8962 *M. lucifugus* banded) and at Wind Cave from 1962 to 1964 (3701 banded). In addition, Davis (1963) netted 4176 *M. lucifugus* at Dixon Cave in the autumn of 1963. When swarming activity was high in August and September, several hundred *M. lucifugus* were captured at cave entrances each night but few were found roosting in the caves in the daytime.

Few *M. lucifugus* were captured more than once at the same cave during a single autumn season. The swarming bats left the area quickly, with individuals remaining at a cave for only a few days at most. However, our data indicate that little within-season shifting from one cave to another occurred. Only one individual was taken at two swarming caves during one season. This was a male netted at Wind Cave on 20 April 1963 and re-netted at Dixon Cave on 1 September 1963 and at Wind Cave on 4 September 1963. Many bats swarmed at the same cave in successive years. Small numbers of bats were found swarming at other caves during the succeeding autumn. Four bats netted at Wyandotte Cave and one at Wind Cave were netted again at other caves about a year later. We infer from these data that during swarming young bats may learn the location of a suitable hibernaculum but most bats do not learn of alternative winter sites in other caves.

Large numbers of *M. lucifugus* netted at Wyandotte and Wind caves in the autumn were found hibernating in the same cave that winter or in subsequent winters. A few (14 from Wyandotte and one from Wind) wintered in caves other than their swarming sites.

Bats from the Indiana nurseries apparently concentrated their swarming activity at Indiana caves, moving mainly to the northernmost of the three swarming sites examined. Summer-to-autumn and within-autumn movements of females from nurseries included 17 recaptures at Wyandotte Cave (nine from Tunnelton and one or two each from six other nurseries), two at Wind Cave (from Tunnelton), and one at Dixon Cave (from Tunnelton). Only 15 per cent of these movements were to Kentucky caves, and probably most of the *M. lucifugus* swarming at Wind and Dixon caves were summer residents from Kentucky and extreme southern Indiana. Davis (1963), in citing recaptures of our nursery-banded bats,

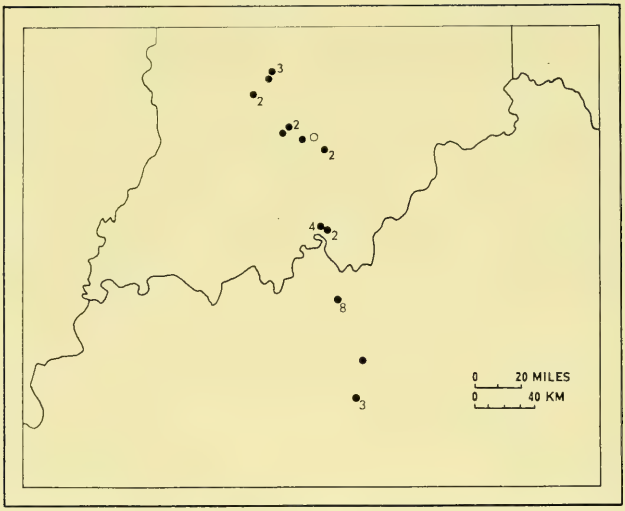

FIG. 6. Foreign recaptures in any winter of *M. lucifugus* of both sexes banded at the Tunnelton nursery (open circle) in autumn.

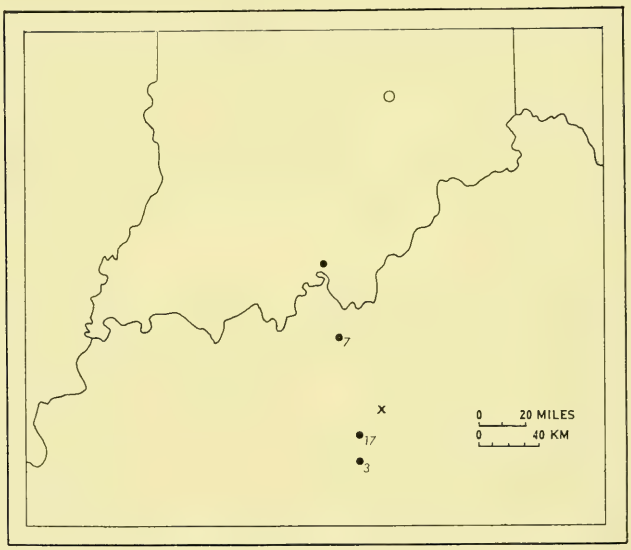

FIG. 7. Foreign recaptures in any winter of *M. lucifugus* of both sexes banded at the Newbern nursery (open circle) in autumn. "X" indicates a citizen recapture.

FIG. 8. Secondary dispersal of female and male *M. lucifugus* banded while swarming at Wyandotte Cave (closed circle). Nurseries shown (open circles) are Tunnelton and Thorntown.

probably overemphasized the contribution of Indiana nurseries to Dixon Cave swarming. None of the 11 bats banded at Indiana nurseries in summer or autumn and recaptured at Dixon Cave was taken in the same year; five of these were banded in autumn and their apparent migration possibly was distorted by other movements, such as dispersal, prior to banding.

A number of *M. lucifugus* netted while swarming exhibited a secondary dispersal by moving away from the swarming cave, mainly in a northerly direction. Secondary dispersal of 13 females and 17 males is shown in Fig. 8. Males appear to move shorter distances from the cave regions than do females. Both sexes showed a strong tendency to move to the Tunnelton nursery. Secondary dispersal probably includes a wider variety of nursery roosts than we recorded, because we did not sample many nurseries

at the appropriate times. Trips from Wyandotte Cave to Tunnelton, 60 kilometers away, were made in one night by several females and males. For example, a male netted at Wyandotte on the evening of 4 September 1963 was captured the next afternoon in the Tunnelton roost. A female netted at Wyandotte on 18 August 1964 was recaptured in the Thorntown barn on 26 August 1964, 209 kilometers to the north. Only three such records were obtained from bats netted at the two Kentucky caves. A female netted at Wind Cave on 1 September 1963 was 143 kilometers to the north at Columbus, Bartholomew Co., Indiana, on 7 September 1963. A male moved 109 kilometers north from Wind Cave to Tunnelton between 1 and 15 September 1963. Davis (1963) cited a female that he banded at Dixon Cave on 30 August 1963 and we recaptured at Tunnelton on 5 September 1963, 174 kilometers to the north. Bats participating in secondary dispersal presumably also perform secondary migration before winter.

The degree to which individual *M. lucifugus* move from one cave to another in winter is not well understood. Griffin (1940*a*, 1945) cited two winter inter-cave movements in Massachusetts, each with the second capture in April. If the recaptures occurred during warm weather, they should be considered spring records. In Indiana, a variety of movements are associated with spring migration and swarming at caves, making cave recaptures from winter to April difficult to interpret. Hitchcock (1965) reported a 113-kilometer, one-day movement of a male in December but suggested that the apparently anomalous record resulted from a record-keeping error. Fenton (1970) recorded two winter changes of hibernaculum by males, one between October and December and one between November and March. Eight within-winter movements recorded in the present study ranged from one to 220 kilometers. Some were from one cave to another, but several citizen recaptures were from non-cave locations. Three other winter recaptures (see chapter on Survival and Mortality) indicate that some bats moving at this season fail to relocate a satisfactory roost or move away from the cave region altogether. These data confirm that individuals move about during winter and occasionally succumb to the harsh conditions encountered.

Records of change of hibernaculum in *M. lucifugus* from one

year to another are common but not abundant (Griffin, 1940*a*, 1945; Myers, 1964; Fenton, 1970). Twenty-four such cases were documented in this study. Seven were females and 17 were males, which is similar to the proportion in which the sexes were banded. No difference existed between the sexes in tendency to shift wintering location.

Few data are available to elucidate spring movements. Our records of winter-to-spring and within-spring movements reflect spring "staging" activities, dispersal, and migration. Staging activities include marked increases and decreases in cave populations (Davis and Hitchcock, 1965), cave-to-cave movement in early spring, and nocturnal flight in and out of caves similar to swarming behavior in autumn. Spring dispersal is generally northward, with some divergence to the east and west. Our data for spring migration suggest a simple cave-to-nursery pattern, with no indication of the more complex movements that occur in the autumn.

In sharp contrast to the variety and complexity of movements at other times of the year, female (and some male) *M. lucifugus* exhibit a high degree of attachment to a nursery site in summer. The only female that moved from one nursery to another within a summer went from Cicero to Tipton, Tipton Co., Indiana (a citizen report at a nursery new to us), between 9 June and the week of 19–25 July 1964. The recapture date is so close to the beginning of autumn movement that such activity may have been involved here. Among 2841 adult and immature females banded in summer, no recaptures during any subsequent summer occurred at other than the original nursery. No males moved from one nursery to another during the same summer, and only one male exhibited such a shift between one summer and another (from Macy on 24 July 1959 to Etna on 20 July 1960). Because only 271 adult males were banded in the summer, it is difficult to judge from the movement data alone whether males are typically restricted to a home roost.

To quantify a bat's tendency to reside year after year in the same roost, we employed a site attachment index:

$$\frac{\sum\left(\frac{Y_r}{Y_p}\right)}{n},$$

TABLE 1

NURSERY SITE ATTACHMENT OF *M. lucifugus*.

Sample site	Banding date	Sample size	Number recaptured	Maximum number of recapture-years	Site attachment value
	Females of all ages				
Tunnelton	30 August 1954	156	46	10	0.54
Tunnelton	1 October 1954	29	9	13	0.64
Tunnelton	7 August 1957	288	98	10	0.81
Tunnelton	14 August 1957	228	59	7	0.72
Franklin	30 July 1959	365	176	4	0.81
Franklin	22 August 1960	219	107	3	0.85
Mean					0.78
	Males of all ages				
Tunnelton	30 August 1954	73	11	11	0.59
Tunnelton	1 October 1954	151	25	8	0.79
Thorntown	19 August 1959	33	11	5	0.67
Mean					0.71
	Adult females				
Tunnelton	20 April 1955	278	127	8	0.59
Etna	20 July 1960	60	7	3	0.81
Pine Village	28 July 1960	57	9	2	0.89
Thorntown	3 August 1961	125	36	4	0.71
Mean					0.64
	Adult males				
Tunnelton	4 July 1956	54	15	9	0.89
Tunnelton	29 May 1958	17	3	5	0.80
Thorntown	3 August 1961	17	6	3	0.89
Mean					0.88
	Immature females				
Etna	20 July 1960	73	8	3	0.90
Camden	25 July 1960	17	4	2	0.88
Thorntown	3 August 1961	89	12	5	0.61
Tunnelton	25 July 1962	175	34	6	0.79
Mean					0.77
	Immature males				
Tunnelton	25 July 1962	151	15	6	0.69
Tunnelton	30 July 1964	96	2	4	0.62
Mean					0.68

where Y_r is the number of years an individual was recaptured at the banding site and Y_p is the number of recapture-years possible in the individual's history. Calculated values were from large samples of bats that were banded early in the study and thus had long histories of recapture opportunity. The attachment index is independent of mortality rate because it includes only the individuals recaptured at the banding site and uses as the denominator only the number of recapture-years possible until an individual's last recapture. The index is a function of the probability of the individual being at the banding site at a similar time each year and of our capture efficiency, which depended on the proportion of the population captured in each sample and the number of samples taken at the site each year. Captures were always less than 100 per cent, resulting in underestimation of site attachment. Capture efficiency in a single nursery visit rarely exceeded 50 per cent but was improved by sampling repeatedly.

Nursery site attachment values are given by age and sex in Table 1. The mean values, ranging from 0.64 to 0.88, were high considering our low capture efficiency and demonstrate that the bats have a strong tendency to return to the same nursery year after year. The high index values for males show that, while most seldom or never visit nurseries, a few males not only prefer nurseries but also have strong attachment to a particular one.

POPULATION SIZE AND FLUCTUATIONS

Nursery Populations

The 50 nurseries examined varied in size from about 20 to 3000 adult females and young, but most populations ranged from 300 to 1200 bats. Nursery populations farthest from hibernacula, in the northern part of the study area, contained relatively few bats; the largest nurseries were near the caves. At most nurseries we estimated population size while obtaining samples from the roost sites, by judging the total number of bats present or adding the sample size to an estimate of the number that escaped sampling. Such visual estimates were not accurate because some bats were inaccessible between boards and shingles, behind beams and rafters, or down in the walls of the building. The proportion of bats that was inaccessible depended on roost temperatures at the time of sampling and on the frequency of disturbance in previous weeks or months. In addition, even experienced observers demonstrated fairly consistent individual bias in estimating numbers. Despite these difficulties, visual estimates give a view of relative nursery size and form the basis for later discussion of population declines. To determine the actual numbers of animals undergoing various processes, we obtained more accurate data on numbers by counting bats as they left their roosts at dusk. Bat flight counts have been made infrequently in the past; previous applications of the technique have been cited by Humphrey (1971).

We conducted flight counts at the Thorntown and Pennville nurseries, where vision was not obstructed by trees surrounding the exits and two observers could see almost all bats that flew. Bats flew from the Thorntown house and barn directly to a pond; three per cent did not go to the pond and were not included in the counts. Bats flew from the Pennville house to a stream. A few bats resided under the roof of an addition to the house and, when exiting, were not visible to the usual two observers. These comprised three to seven per cent of the total population and were

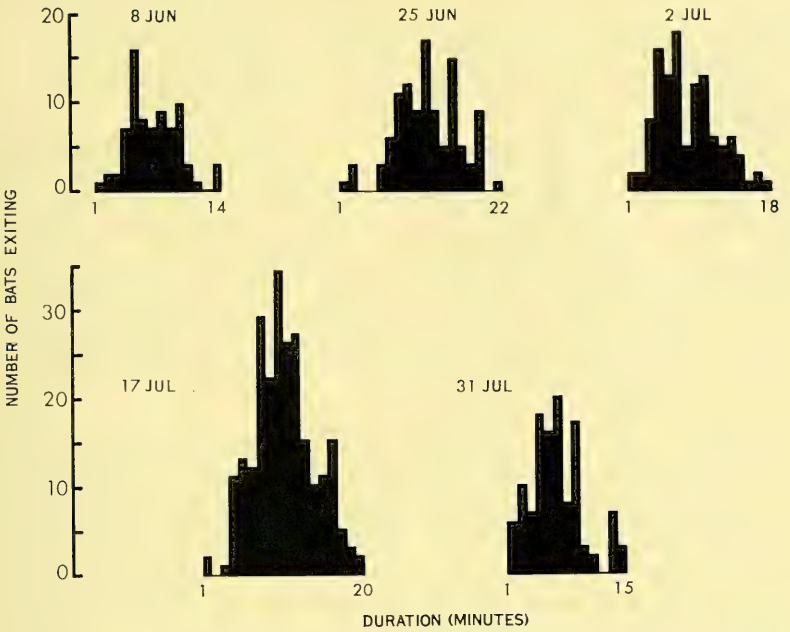

Fig. 9. Evening emergence patterns of *M. lucifugus* from the Thorntown house in 1964.

not included in the counts. Evening departures of bats from the roost were more or less normally distributed but showed irregularities resulting from brief bursts of activity between short inactive periods (Fig. 9). Departure periods were of short duration and few bats were missed because of darkness. The slow exit rate simplified counting individuals. Post-flight checks of the roosts in early June, late July, and August showed that few volant individuals failed to leave the roost. We did not check during or shortly after the parturition period. Post-flight sounds suggested that flights were not complete during this time, so some bias is expected.

In 1964, visual estimates of abundance at the Thorntown nursery (Fig. 10) showed no readily interpretable pattern until mid-August when they were adjusted to agree with our first flight counts. In 1965, we made flight counts about once a week to monitor changes in population size. Bats arrived from April to

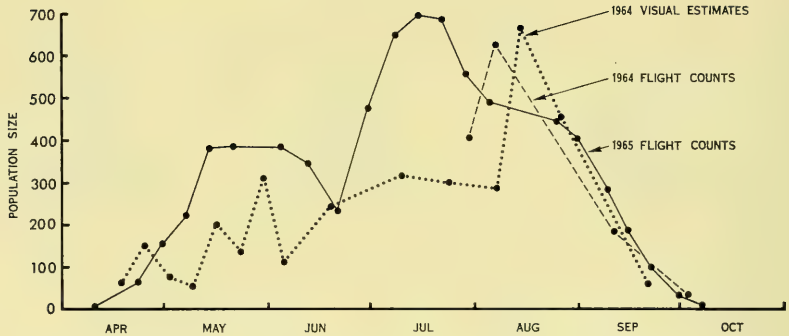

FIG. 10. Changes in *M. lucifugus* population size at the Thorntown nursery.

mid-May, when the population stabilized at about 400 adults. A decline to about 380 bats began in early June just prior to parturition, possibly because transient animals moved out. The lowest count in June was probably biased by cool and windy flight conditions. An increase in numbers corresponding with recruitment of young into the volant population began in early July and peaked in mid-July. This was followed by a decline in late July, a plateau in August, and a steady decrease in September, ending in October.

Weekly counts at another nursery in 1965 exhibited approximately the same pattern (Fig. 11). A stronger decline occurred following the May build-up, suggesting that more transient animals moved through this colony. To see if we were missing day-to-day variation, the 1966 counts here included daily counts in June, July, and August. The 1966 peak was brief and could have been missed if only weekly counts had been made. The early July low of 570 could not have accounted for the subsequent peak of 1360 even with 100 per cent reproduction, suggesting that during the parturition period some females did not join the early evening flight. Marked daily variation occurred during migration, raising the question of whether bats moved away from the nursery in groups.

Flight counts are sensitive to disturbance effects. The 1965 curve (Fig. 11) shows declines after sampling in early June and mid-July. Declines were to be expected at these times, but the disturbance of sampling appeared to accentuate this

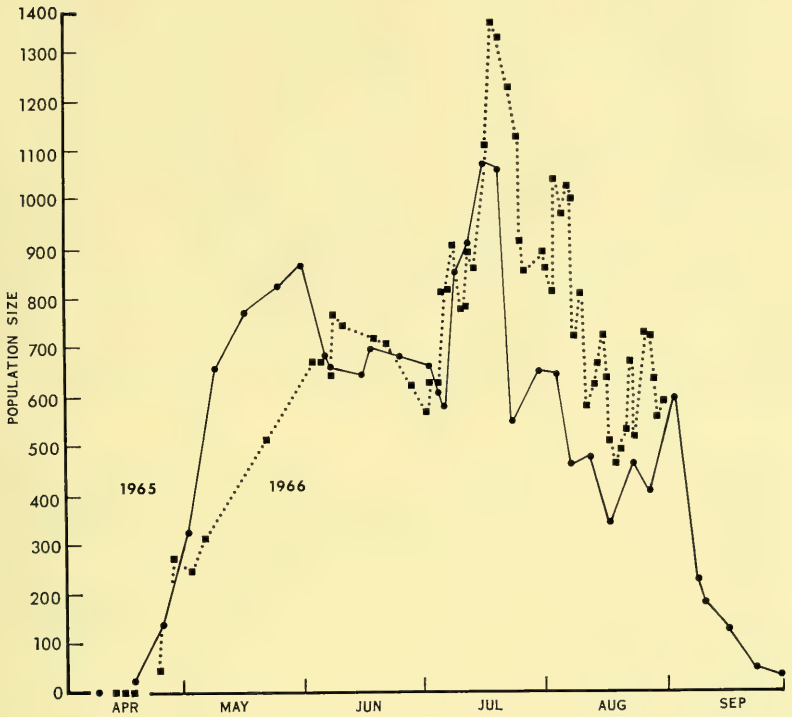

FIG. 11. Changes in *M. lucifugus* population size at the Pennville nursery.

trend. A sample taken in early July did not prevent the increase in numbers expected from the flight of young. Weekly sampling disturbance in the Thorntown house in 1964 caused most of the bats to move to the barn roost. When sampling frequency was reduced, many of the animals returned to the house. Such disturbance effects could be minimized by sampling less often (not more than once a month) or possibly could be avoided by using exit traps in the evening (Griffin, 1940*a*; M. D. Tuttle and T. H. Kunz, personal communication).

Applying the Thorntown population size curve to pooled sample data provides an indication of trends in nursery population structure during the summer (Fig. 12). These data suggest that about 350 adult females stayed in Thorntown in June. With a litter size of one and an average pregnancy rate of 98

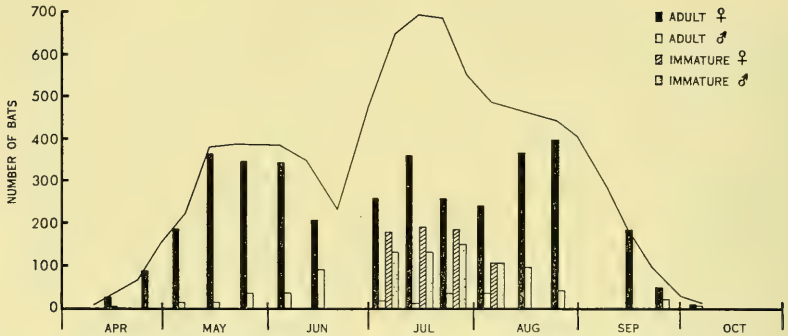

FIG. 12. Changes in population size (line, from Fig. 10) and structure (pooled samples, 1958 to 1969) of *M. lucifugus* at the Thorntown nursery.

per cent, these females would be expected to produce 343 young. Counts of about 695 bats in mid-July, associated with observations of low postpartum mortality, agree with this expectation. The counts further indicate that the females did not leave the nursery as soon as their young were weaned. Adult females began to leave in late July, and young of both sexes began to depart in early August.

Swarming Groups

One part of the migratory activity pattern of *M. lucifugus* was monitored by mist-netting at cave entrances. This method does not provide data that can be related to nursery or hibernaculum population sizes. The number of individuals captured simply reflects the number of bats present at that particular time and place. More bats were caught at the entrance than could be found in the cave either earlier that day or on the following day. Thus many of the bats moving through the cave entrances were spending the day roosting in the surrounding area or were arriving from more distant sites.

The scanty spring netting data from Wind, Wyandotte, and Donnehue's caves show that swarming activity (in comparison to autumn levels) is low in the third week of March (Wind), moderate in the second week of April, high in the third week of April and the first week of May, moderate in the second

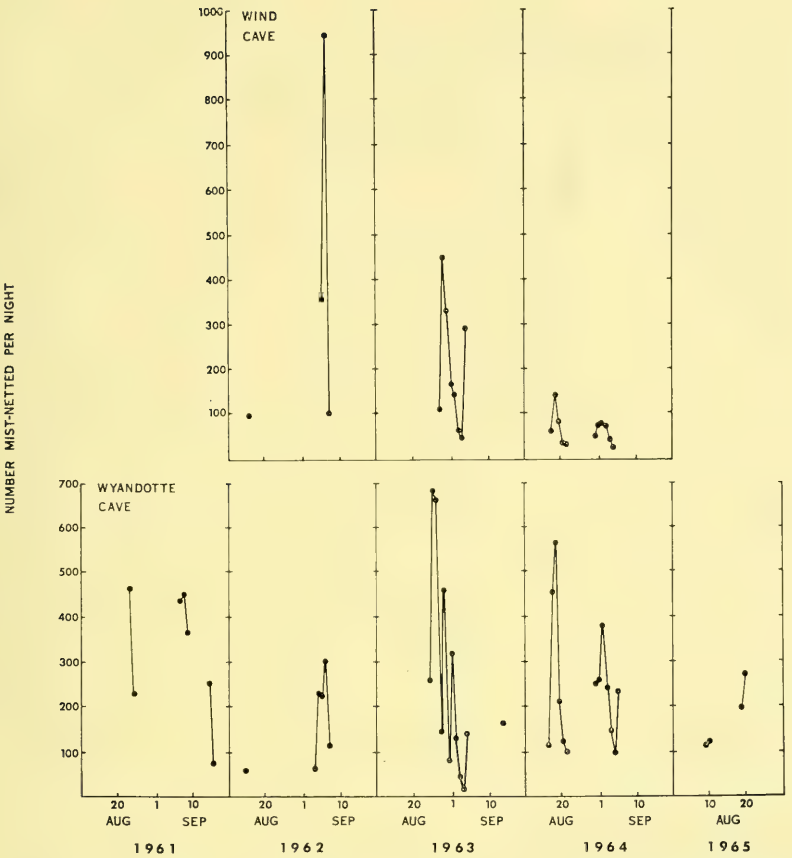

Fig. 13. Number of *M. lucifugus* mist-netted per night during autumnal swarming at Wind Cave and Wyandotte Cave.

and fourth weeks of May, and low in the first week of June. In the last week of July, when adult females begin to leave the nurseries, activity was moderate at Wyandotte Cave.

The extent of swarming in August and September at Wyandotte and Wind caves is summarized in Fig. 13. Later in the autumn, swarming activity at Wyandotte Cave was moderate in the second week of October and light in the third. The numbers of *M. lucifugus* caught each night varied markedly, and activity at the two caves was apparently synchronous. High levels of

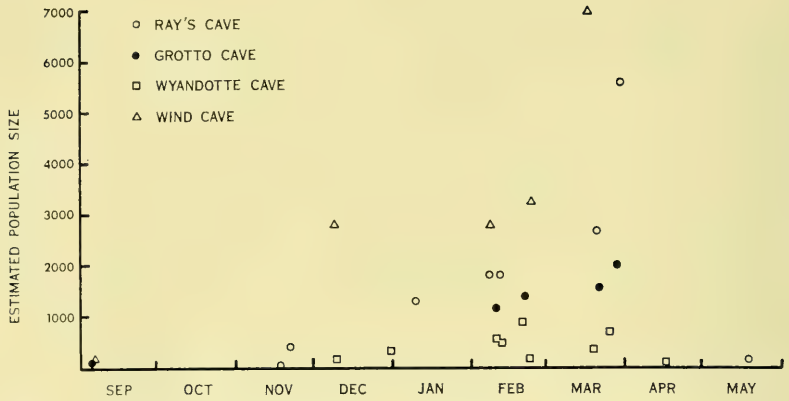

FIG. 14. Population size estimates of hibernating *M. lucifugus* in four caves.

activity occurred at both caves on 6 September 1962, 19 August 1964, and 2 September 1964, whereas few bats were swarming at either cave on 3 September 1963. Correlation of extreme levels of activity from year to year suggests a similar annual pattern for autumn swarming. A substantial decrease of the overall level of activity occurred at Wind Cave following a flood in March 1964 (DeBlase *et al.*, 1965), indicating that the majority of *M. lucifugus* swarming at Wind Cave also winter there or perhaps at other caves that also flooded.

Winter Populations

Estimates of torpid bats in winter were based on actual numbers captured plus estimates of numbers of animals too high or too deep in crevices to be reached. Sources of error included individual bias in estimating numbers and the difficulty of distinguishing *Myotis sodalis* from *M. lucifugus* at a distance. When we recognized that *M. lucifugus* usually formed loose clusters and *M. sodalis* formed dense clusters, the latter source of error diminished.

Winter population estimates were made too infrequently to give a clear picture of winter population trends. Because we assumed that few population changes took place in winter and wished to avoid arousing torpid bats any more than was necessary, usually only a single population estimate was made for a cave

each winter. Combination of these values, however, suggests that hibernating populations change markedly during the winter (Fig. 14). Numbers appear to increase from November through March and decrease in April and May.

Few authors have presented data on *M. lucifugus* population changes during a single winter. At Tyendinaga Cave, Ontario, Hitchcock (1965) observed 58 on 17 January 1941 and 125 (including only 13 from the previous group) on 17 April 1941. Folk (1940) found that a population at Indian Oven Cave, New York, increased until January, fluctuated in January and February, and decreased in late February. Although almost all of the bats he examined were *M. lucifugus*, he did not separate three other species in reporting bat numbers. Davis and Hitchcock (1965) reported a large and stable population in a mine in New York, in February and March, followed by a decline in May. Although he gave no data, Griffin (1945) reported that an autumn hibernating population of several hundred *M. lucifugus* at Aeolus Cave, Vermont, was reduced to fewer than 50 in mid-winter by freezing roost area temperatures. Extremely cold roost temperatures were not recorded in the present study. Davis and Hitchcock (1965) found several hundred *M. lucifugus* in the Aeolus Cave roost site at various dates between September and March in several years and noted a population buildup and decline involving 2500 to 3000 *M. lucifugus* in April and May. The latter trend probably reflects spring arousal and migration events to which the data of the present study are not sensitive.

If, as the data suggest, major changes in *M. lucifugus* population size occur during winter, large numbers of bats must spend portions of the winter undetected. Based on changes of cave populations in spring, Davis and Hitchcock (1965) thought numbers increased in April because bats emerged from inaccessible parts of the cave. All caves in the present study contained such sites, including recesses and passages too small to investigate by conventional means. Bats also might winter in caves unknown to investigators. Davis and Hitchcock presented arguments for rejecting the contention that this species spends the winter in heated buildings, and bats were absent from nurseries at our winter visits. Our winter band returns at buildings were indi-

viduals suddenly appearing in rooms or sheds and apparently involve transient animals, not hibernating individuals. Possibly some bats may winter in rock crevices or hollow trees, but there is no evidence to support this suggestion. Although Griffin (1940*a*) cited Mearns (1898) as finding dormant little brown bats in hollow trees in winter, Mearns' reference was to *Vespertilio subulatus,* which then referred to the species now recognized as *Myotis keenii.*

SEX RATIOS

To highlight seasonal trends in sex ratio, sample data from all years and populations were pooled. Summer samples were grouped in 10-day intervals. Because changes in winter sex ratio were less rapid, 30-day intervals were used. A X^2 test was used to detect the significance of deviations from expected 1:1 sex ratios. If $25 \leq n < 200$, a correction factor was applied to the test (Sokal and Rohlf, 1969). Statistical significance was not tested if $n < 25$.

Nursery Populations

Maturing of the young made it difficult to determine age of all individuals in some samples as early as 22 July, whereas age of every individual could be judged as late as 7 August in other samples. This situation reflects population differences in birth dates and rates of development. Samples taken after adults and young could not be reliably distinguished are analyzed as a third type of sample. Sex ratio values for adult, immature, and unaged samples are summarized in Fig. 15.

Samples of prevolant young did not differ significantly from 50 per cent female (Table 2). The same is true of volant young in early July, but in late July and early August the proportion of females rose significantly because young males were leaving the nurseries earlier and at a more rapid rate than were females. Previously published data (Table 3) show the same pattern for prevolant young but the opposite trend (based on rather small samples) for volant young. Further examination of our data suggests that either the departure pattern shown may be heavily dependent on the sampling schedule used or that departure patterns differ from one population to another. For example, at Thorntown (Fig. 12) no prevolant samples were taken, so the basic ratio is not known. By early and mid-July the volant young were predominantly females, so perhaps males already had begun departure. In late July the departure rate of females began to overtake that of males, and a 1:1 sex ratio occurred in early August.

TABLE 2

PERCENTAGE OF FEMALES AMONG IMMATURE *M. lucifugus* IN INDIANA.

Date	Number of samples	Pooled sample size	Number of females	Per cent female
		Prevolant samples		
1–10 June	1	8	4	50.0
11–20 June	0			
21–30 June	1	169	82	48.5*
1–10 July	2	240	120	50.0
11–20 July	1	492	245	49.8
Total	5	909	451	49.6
		Volant samples		
1–10 June	1	4	3	75.0
11–20 June	1	1	1	100.0
21–30 June	1	1	0	0.0
1–10 July	7	504	248	49.2
11–20 July	6	269	149	55.4
21–31 July	22	2203	1227	55.7**
1–10 August	16	1406	845	60.1**
Total	54	4388	2473	56.4**

* Significant ($P < 0.05$).
** Highly significant ($P < 0.01$).

Although the immature sex ratio data of Smith (1954, 1957) extend farther into autumn than other data, these values are of doubtful reliability because Smith determined age by tooth wear. Hall *et al.* (1957) considered tooth wear an unreliable age indicator for *M. lucifugus* because the canine teeth of four bats 18 to 19 years old were only slightly worn. We also observed canines with little or no wear in banded *M. lucifugus* up to 14 years old.

Adults in nurseries consisted almost entirely of females (Table 4). Almost no adult males were present in early spring but their proportion increased through May and June, reaching 8.4 per cent in late July and early August. At Tunnelton, a large southern nursery, the proportion of males was generally higher, reaching an average of 18.2 per cent in four samples in July. Because Tunnelton samples made up a large portion of the adults examined in certain 10-day intervals, actual proportions

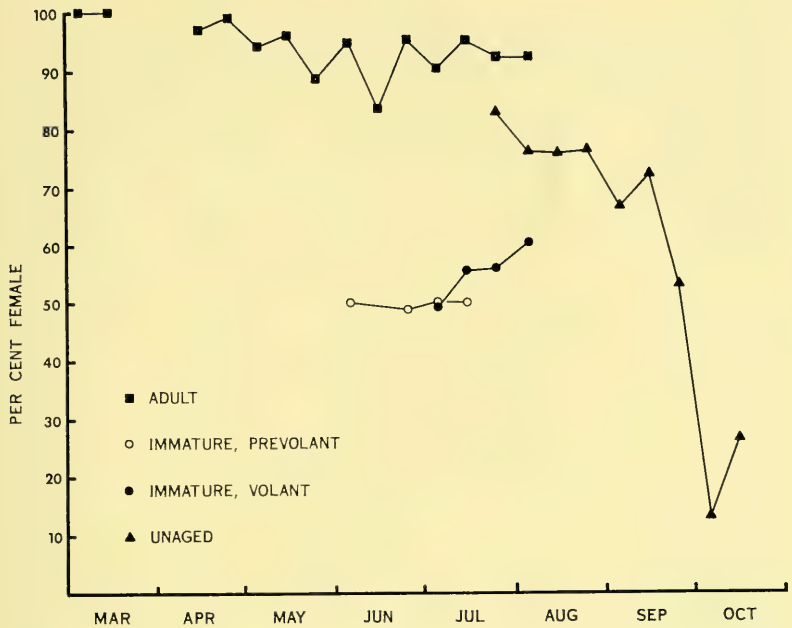

FIG. 15. Average percentage of female *M. lucifugus* in Indiana nurseries.

of males in more northerly nurseries may be much lower than suggested by Table 4. Possibly most males do not move as far away from the cave area in summer as do females.

Similar seasonal patterns in adult sex ratios at nurseries occur in published data from other regions (Table 5). In most studies the frequency of males is highest in June and July. Few reliable August data are available because of the difficulty of determining age by that time. The data in Table 5 show that adult males are more prevalent in nurseries near the southern limits of distribution than those in the center of the range of the species.

The dramatic reversal of sex ratio in unaged nursery samples in the autumn (Fig. 15) reflects both migration and the transient visitation discussed previously. Some departing mothers and young were replaced by transient bats that were predominantly males (Humphrey and Cope, 1964). Presumably visiting bats were from both summer shelters and other nurseries. In October, when most resident animals were gone, most (86.1 per cent) of

TABLE 3

PUBLISHED DATA ON PERCENTAGE OF FEMALES AMONG IMMATURE *M. lucifugus*.

Reference	Date	Sample size	Number of females	Per cent female
	Prevolant or probably prevolant			
Allen, 1921	5 July 1907	101	53	52.5
Cagle and Cockrum, 1943	18 May–12 July 1940	153	80	52.3
Total		254	133	52.4
	Probably prevolant and volant			
Griffin, 1940*b*	summer	890	440	49.4
	Volant or probably volant			
Davis and Hitchcock, 1965	7–8 July 1960	119	64	53.8
Dymond, 1936	7–13 July 1934	54	19	35.2*
Dymond, 1936	17 July 1933	25	6	24.0**
Stegeman, 1954*a*, 1954*b*	14–15 July 1949	257	123	47.9
Benton and Scharoun, 1958	22, 30 July 1955	108	53	49.1
Smith and Goodpaster, 1956	18 August 1955	27	4	14.8**
Total		590	269	45.6*

* Significant ($P < 0.05$).
** Highly significant ($P < 0.01$).

a sample of 310 bats were males. This influx of males was strong at nurseries such as Tunnelton, near the caves used for swarming and hibernation, whereas the effect was less pronounced at more distant nurseries. For example, males increased to only 31.6 per cent of 52 sampled at Thorntown in late September and October. The function of this behavior is unknown.

Shelter Groups

Shelters housed mostly adult males in early summer, but adult females and young of both sexes appeared in late July and August. Published data on sex ratios of adult *M. lucifugus* in shelters show a similar preponderance of males (Table 6). Many farmers in Indiana commented that they occasionally observed single bats roosting in a barn or other building for a few days. Some of these were no doubt *Eptesicus fuscus*, but

TABLE 4

PERCENTAGE OF ADULT FEMALE *M. lucifugus* IN ALL INDIANA NURSERIES AND AT THE TUNNELTON NURSERY (IN PARENTHESES).

Date	Number of samples	Pooled sample size	Number of females	Per cent female
1–10 March	1(1)	1(1)	1(1)	100.0(100.0)
11–20 March	1(1)	1(1)	1(1)	100.0(100.0)
21–31 March	0			
1–10 April	0			
11–20 April	3(2)	452(428)	438(415)	96.9(97.0)
21–30 April	3(1)	80(51)	79(50)	98.8(98.0)
1–10 May	4(1)	394(296)	370(277)	93.9(93.6)
11–20 May	3(0)	138	132	95.7
21–31 May	3(1)	280(205)	247(179)	88.2(87.3)
1–10 June	8(2)	769(195)	726(167)	94.4(85.6)
11–20 June	2(1)	107(74)	89(66)	83.2(89.2)
21–30 June	2(0)	480	456	95.0
1–10 July	10(2)	908(702)	815(600)	89.8(85.5)
11–20 July	5(0)	609	577	94.7
21–31 July	22(2)	2200(729)	2016(570)	91.6(78.2)
1–10 August	16(0)	1804	1652	91.6
Total	83(14)	8223(2682)	7599(2326)	92.4(86.7)

TABLE 5

PERCENTAGE OF FEMALES AMONG ADULT *M. lucifugus* IN NURSERIES IN JUNE AND JULY IN VARIOUS GEOGRAPHIC AREAS.

Reference	Location	Number of samples	Pooled sample size	Number of females	Per cent female
Dymond, 1936	Ontario	3	64	64	100.0
Davis and Hitchcock, 1965	Vermont	4	880	831	94.4
Stegeman, 1954*a*, 1954*b*	N New York	2	353	353	100.0
Benton and Scharoun, 1958	SE New York	1	62	62	100.0
Allen, 1921; Wimsatt, 1945	W New York	2	185	177	95.7
Smith, 1954	NE Ohio	42	1109	1081	97.5
This study	Central Indiana	42	3373	3276	97.1
This study	S Indiana	7	1700	1403	82.5
Davis *et al.*, 1965	E Kentucky	6	2379	1827	76.8
Davis *et al.*, 1965	SW Kentucky	1	94	62	65.6
Cagle and Cockrum, 1943	S Illinois	6	288	225	78.1

TABLE 6

PERCENTAGE OF MALES AMONG *M. lucifugus* TAKEN IN SUMMER SHELTERS IN JUNE.

Reference	Location	Number of samples	Pooled sample size	Number of males	Per cent male
Davis and Hitchcock, 1965	Vermont, cave	3	648	632	97.5
Davis and Hitchcock, 1965	New York, mine	1	63	55	87.3
Krutzsch, 1961	West Virginia, cave	1	40	40	100.0
Myers, 1964	Missouri, cave	?	6	6	100.0
This study	Indiana, cave	2	5	5	100.0
Miller, 1955	Michigan, shutters	40	82	70	85.4
This study	Indiana, pavilion	1	3	3	100.0
Glass and Ward, unpublished	Oklahoma, siding	1	10	10	100.0
This study	Oklahoma, siding	1	7	7	100.0
Total		51	864	828	95.8

clearly many adult male *M. lucifugus* spend the summer singly in transient roosts or in small groups at permanent sites (see Miller, 1955).

Swarming Groups

Mist-netted samples at cave entrances showed considerable variation in sex ratios. Usually night-to-night changes in numbers caught were in the same direction and of approximately the same magnitude for both sexes, but occasionally large numbers of one sex arrived or departed with little apparent change in numbers of the other.

Sex ratios of swarming *M. lucifugus* are presented in Table 7. In middle and late April, about 65 per cent of the bats active at cave entrances were females. At the same time the proportion of females torpid in caves (Fig. 16) was dropping and females were arriving at nursery roosts. By mid-May, few females remained in the caves and the proportion of females swarming

TABLE 7

PERCENTAGE OF MALES AMONG SWARMING *M. lucifugus* MIST-NETTED AT CAVE ENTRANCES (DONNEHUE'S, RAY'S, WYANDOTTE, AND WIND) IN INDIANA AND KENTUCKY.

Date	Number of net nights	Total sample size	Number of males	Per cent male
11–20 March	2	5	3	60.0
21–31 March	1	0		
1–10 April	0			
11–20 April	4	544	184	33.8
21–30 April	5	275	103	37.5
1–10 May	2	153	118	77.1
11–20 May	3	63	53	84.1
11–20 July	1	38	32	84.2
21–31 July	3	228	180	78.9
1–10 August	2	238	159	66.8
11–20 August	12	2371	1430	60.3
21–31 August	24	5386	3411	63.3
1–10 September	29	7340	5569	75.9
11–20 September	4	556	415	74.6
21–30 September	0			
1–10 October	1	7	5	71.4
11–20 October	3	270	219	81.1

was diminishing rapidly. At this time most females were present in the nurseries in central Indiana (Figs. 10 and 11).

Throughout the autumn swarming period, more males than females were caught at cave entrances. The percentage of males dropped from 84 in mid-July to 60 in mid-August and then rose to 81 in mid-October. Fenton (1969*a*) reported a similar decline in the August values when immatures, whose sex ratio was closer to parity than that of adults, began to outnumber adults. Similar patterns appear also in the data of Davis and Hitchcock (1965) and Hall and Brenner (1968). A given sex ratio occurred at Wind Cave from four to 10 days earlier than at Wyandotte Cave in spring and autumn, a pattern that makes phenological sense only in the spring.

Winter Populations

Sex ratios of hibernating *M. lucifugus* in Indiana and Kentucky caves are presented in Fig. 16. Males were always more abundant

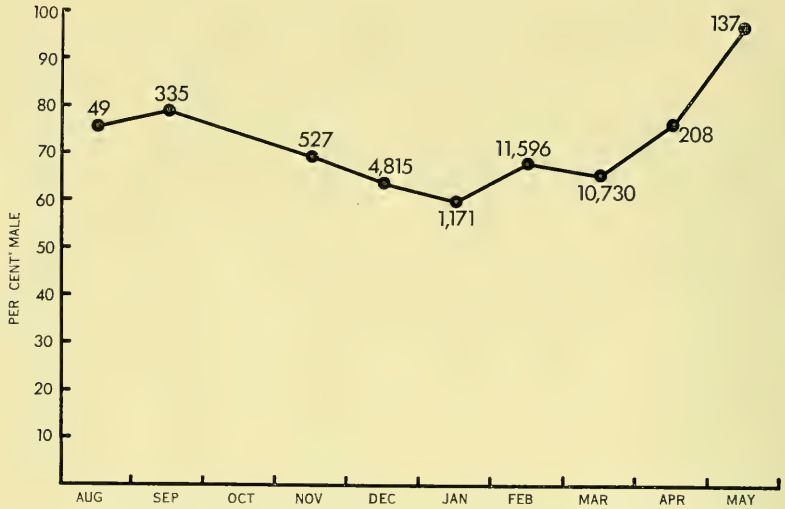

FIG. 16. Average percentage of males among *M. lucifugus* hibernating in Indiana and Kentucky caves. Numbers indicate monthly sample size.

than females. Sex ratios were closest to parity in mid-winter and most unbalanced in favor of males in August, September, April, and May. The high percentage of hibernating males in September coincided with a high percentage of males among swarming bats (Table 15) and with continued decline in the number of females at nurseries. The location of large numbers of females at this time is not known. The increased proportion of males in hibernating bats in late April corresponded with a low proportion of that sex among swarming bats and with arrival of females at nurseries. By mid-May almost no females were hibernating and few were flying in and out of the caves.

Many authors have reported disproportionate sex ratios in hibernating *M. lucifugus* without specifying sampling dates (Griffin, 1940*b*; Wimsatt, 1945; Hitchcock, 1950; Layne, 1958; Muir and Polder, 1960; Moisan, 1961; Pearson, 1962; Myers, 1964; Heltsley, 1965). Males comprised 68.1 per cent of the hibernating populations in these studies. In view of the marked changes in sex ratio occurring in winter in Indiana and Kentucky, probably no small group of samples can be used to obtain a "typical" winter sex ratio in this species. Instead,

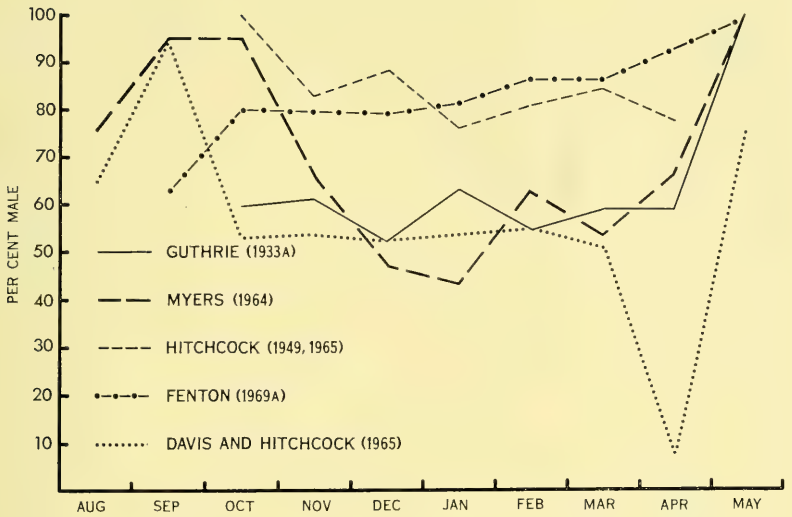

FIG. 17. Average percentage of males among hibernating *M. lucifugus* based on published data.

long series of samples need to be examined to ascertain trends in winter sex ratio. Monthly averages of five such sample series are plotted in Fig. 17. The differences shown are probably not as pronounced as they appear, as the uneven sampling effort during the winter typical of these and the present studies yield somewhat misleading results. This is especially true of the months of August, September, October, April, and May, when changes in numbers and sex ratios occur rapidly. For example, all but two of the studies had only small or no samples in April and thus could not have been sensitive to sex ratio changes associated with staging and departure from hibernacula. Davis and Hitchcock (1965) found rapidly shifting sex ratios from early April to mid-May. These were caused by a great increase in the number of females through April, followed by a decrease in May and by an increase in the number of males in early May. Because relatively few *M. lucifugus* apparently occupied this roost earlier in the winter, the addition of bats of predominantly one sex had a strong impact on the sex ratio. The May samples reported by Hitchcock (1949, 1965) were from both minor and major hibernacula. His samples were all

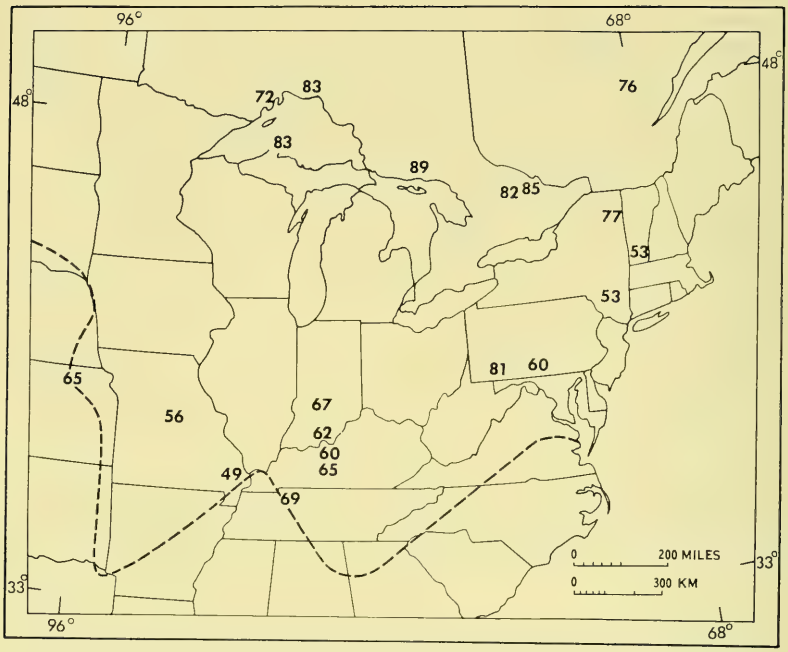

FIG. 18. Average percentage of males among hibernating *M. lucifugus* in this and other studies, pooled samples from November through March. Dashed line is southern limit of distribution. Data are from Moisan (1963); Hitchcock (1949, 1965); Fenton (1970); Allin (1942); Hinckley (unpublished); Davis and Hitchcock (1964); Davis and Hitchcock (1965); Mohr (1945); Hall and Brenner (1968); Smith (1954); Mahan and Lewis (unpublished); Myers (1964); Guthrie (1933*a*); Fitch (1966); and this study.

from the early and middle portions of the month and showed no substantial change in sex ratio. All studies of May samples yielded high proportions of males, indicating that males were typically slower to leave hibernacula in spring than females.

The other distinctive feature of major winter studies (Figs. 16 and 17) is a mid-winter period of relative stability in sex ratio. Each cave or group of hibernacula seems to have its own characteristic mid-winter sex ratio. Hitchcock (1950) and Fenton (1970) have suggested that the more southerly hibernacula typically contain higher proportions of females than do those to the north. Fig. 18 presents the percentage of males in samples

from November through March in various regions. Pooled samples smaller than 50 are excluded. The interval December through February has somewhat more stable sex ratios but excludes many of the published data. Data from the present study are grouped into four north-to-south units. Northern hibernacula usually do have higher proportions of males. However, exceptions to this pattern occur, notably the large populations in Vermont and southern New York.

The rising proportion of females in early and mid-winter, the increasing cave populations during the winter, and the numerical dominance of males in caves despite higher survival of females (see below), suggest that many females are absent from the caves (or cave areas accessible to investigators) at the beginning of winter. These appear to trickle into the sampling sites during the season, most being present by the coldest months.

REPRODUCTION AND DEVELOPMENT

Age at Sexual Maturity

Apparently females are sexually mature in their first autumn and bear young at the age of one year. At least some young males also appear to become sexually mature by the first autumn. Fenton (1969*b*) observed young of both sexes copulating in autumn, and Davis and Hitchcock (1965) noted that unbanded yearling females were pregnant. These authors determined age by the shape of the finger joints up to five (Fenton) and 11 (Davis and Hitchcock) months.

Unfortunately, other studies of the age at sexual maturity have relied partially or wholly on tooth wear as an age criterion (Guthrie, 1933*b*; Miller, 1939; Smith, 1957). Smith (1957) recaptured pregnant bats that had been banded as young a year earlier. Judging from her sampling dates, it is likely that some of these were banded when unmistakably immature. Guthrie (1933*b*) reported the presence of sperm in "young" males and females in winter. Miller (1939) asserted that spermatogenesis did not occur until the second summer. He did not indicate how age was determined other than by sexual development, but he probably relied on tooth wear because his work was directed by Guthrie. Nonetheless, it is likely that at least some of the males with small testes and inactive seminiferous tubules and accessory glands were young.

Rapid sexual maturity in females is important to achieving a high realized natality. Slower development by males would not affect natality, whereas delayed breeding of some males until their second year should maintain selective pressure for successful genotypes.

Breeding Season

Copulation occurs in autumn, winter, and probably spring. A pair of *M. lucifugus* was found copulating in the Thorntown nursery on 20 August 1960. All other observations of copulation have been in caves. Fenton (1969*b*) observed frequent

copulation from the beginning of September through early October. Copulation has also been noted in October (Hahn, 1908; Hall, 1962), November (Griffin, 1940*b*), January (Guilday, 1948), and at various times in winter (Wimsatt, 1945; Fenton, 1969*b*; this study). Winter copulation appears to be infrequent and is usually observed after hibernating bats have been disturbed. However, its occurrence during normal winter arousal periods is likely. Guthrie (1933*b*) recorded copulation in the laboratory at low temperatures in late March. It is probable that insemination often occurs in spring.

Ovulation occurs after the females have left hibernation and before or shortly after they arrive at the nurseries (Wimsatt, 1944*b*). Wimsatt (1945) estimated the gestation period in New York at 50 to 60 days. Guilday (1950) noted a rare case of a female carrying an embryo on 31 January.

Parturition

Parturition generally begins later in the north than in the south. In Ontario, Fenton (1966) recorded the first nursery birth on 9 June, and the first laboratory birth on 7 June and the last on 29 June. Davis and Hitchcock (1965) in Vermont found that one bat each in samples of 114 and 169 adult females on 7 June had given birth, and some females were still pregnant on 10 July. In New England, Griffin (1940*b*) found newborn young from 13 June to 14 July. The parturition period in northeastern Ohio (Smith, 1954) extended from 10 June to 17 July. In Kentucky, Davis *et al.* (1965) found that two of 228 adult females had given birth on 21 May and 14 of 402 were still pregnant on 21 June. Cagle and Cockrum (1943) reported that in southern Illinois two of 173 adult females had given birth by 17 May, whereas one of 46 was still pregnant on 12 July.

The parturition period in Indiana begins in the last week of May and the first week of June. Birth dates vary from nursery to nursery, presumably reflecting the effects of both latitude and roost microclimate. Parturition times also may vary between years, but this was not measured. At the Pennville nursery on 20 May none of 53 reproducing females had given birth; on 5 June 246 reproducing females and eight young were sampled.

One of 59 females had given birth at Pine Village on 8 June 1964, whereas on the same date at Macy, 106 adult females and 53 young were counted. The next day at Cicero 90 adult females and 21 young were captured. At Tunnelton on 9 June 1958 one of 38 reproducing females had given birth as had one of 34 the following day.

Parturition in Indiana ends in the first and second weeks of July. None of 114 females at Milroy-South was still pregnant on 6 July 1965, but one of 127 was pregnant at Pennville on 7 July 1965. On 8 July 1965 at New Castle one of 95 females was still pregnant. At Thorntown none of 33 females on 10 July 1964 and none of 38 on 12 July 1966 was pregnant. Two of 376 females were still pregnant on 13 July 1965 at Reelsville.

Period of Maternal Care

The interval between the first birth and the earliest flying young gives a rough measure of the period of maternal care, although the date of first flight may slightly precede weaning. Under laboratory conditions in Ontario, Fenton (1966) found the first flying young on 25 June 1965, 18 days after the first birth, and considered three weeks a reasonable estimate of the developmental time to flight. Griffin (1940*b*) captured flying young in early July in New England and judged the age at first flight at three weeks to a month. Cagle and Cockrum (1943) recorded the earliest flying young in southern Illinois on 14 June 1940, 29 days after the first birth. In this study, young *M. lucifugus* began to fly at about four weeks of age. On 29 June 1966 a few young at Reelsville could fly. At Milroy-South on 6 July 1965, 144 of 164 young were volant. Three of 40 young were volant on 10 July 1964 at Thorntown. All of 94 young were capable of flight on 21 July 1965 at Milroy-South. On 23 July 1965 at New Castle, 73 of 75 young were volant.

Litter Size and Number of Litters Per Year

Although histological evidence indicates that a litter size of one is typical for *M. lucifugus* (Guthrie, 1933*b*; Guthrie and Jeffers, 1938; Wimsatt, 1944*a*), few authors have cited numbers of near-term fetuses in necropsied females. Mohr (1933) recorded

TABLE 8

ANNUAL REPRODUCTION RATES OF *M. lucifugus* AT INDIANA AND OHIO COLONIES.

Nursery	Date	Number of adult females	Number pregnant	Number pregnant or lactating	Number lactating	Number barren	Per cent reproducing
Tunnelton	9 June 1958	39	37		1	1	97.4
Tunnelton	10 June 1958	35	33		1	1	97.1
Pennville	5 June 1965	251	–	246	–	5	98.0
Pennville	20 May 1969	54	53		0	1	98.1
Milroy-South	5 June 1969	14	–	14	–	0	100.0
Germantown, Ohio	30 June 1969	27	0		27	0	100.0
Total		420	–	412	–	8	98.1

births of single young to three females. Dymond (1936) took single embryos from each of three females and Rysgaard (1942) collected a female with a 10 millimeter fetus. Gates (1936) dissected a female with two embryos, each less than a millimeter long in February; early ovulation presumably was a result of laboratory conditions. Wimsatt (1945) found two females each with two well-developed fetuses. Davis (1967*a*) captured a female with two newborn young and a placental scar in each uterine horn. In the present study, dissection of 13 near-term females revealed only single embryos. As Wimsatt (1945) stated, twinning is probably rare in this species. No more than one litter a year has been reported for this species and no evidence of second litters was found in this study.

Proportion of Breeding Females

The proportion of females reproducing each year is consistently high (Griffin, 1940*b*). Reproductive rates in the nurseries surveyed in the present study ranged from 97.1 to 100 per cent (Table 8). Other published values also are high, averaging 97.4 per cent reproduction in 901 adult females (Cagle and Cockrum, 1943; Smith, 1957; Layne, 1958; Fenton, 1966). Because most values are from samples of near-term or lactating females, the number of reproducing females in a population is approxi-

mately equal to the annual number of births. The only deviation would be caused by stillbirths and late abortions, which have not been reported under natural conditions and probably occur infrequently. Apparently few females are not residing at nurseries during the period of pregnancy and lactation. Females seldom appear at male roosts until nurseries begin to break up. Miller (1955) found a few barren females at a male roost in the reproductive period. A useful check would be to compare the reproductive rates of nursery samples and samples mist-netted at feeding areas.

No extensive data exist on the relation of age and fertility, but the high overall reproductive rate and known cases of successful reproduction in females nine and 12 years old (Hall *et al.*, 1957) suggest little variation with age. The low fertility noted for yearlings (47.8 per cent of 23 yearlings reproducing) by Davis and Hitchcock was not apparent in the populations we studied.

SURVIVAL AND MORTALITY

Survival

SURVIVAL data are from recaptures made during annual visits to banding sites, some recaptures from other seasons, and a few citizen reports. Analysis was based on yearly intervals. Because most visits to a population were not exactly a year apart, any recapture was considered to represent x years survival if it deviated not more than 2.5 months from a date exactly x years after banding. Thus a bat banded in mid-August was recorded as surviving one year if taken any time between June and October the following year. This procedure introduces bias if the accepted deviation period includes significant seasonal variation in survival, as would be the case in the above example if mortality rates were higher in September than in July. On the other hand, considerably greater bias would result from recording 10-month recaptures as representing zero survival.

Recapture rates of many banded cohorts were low because of extermination, low sampling success, or failure to visit populations in some years. Under these circumstances many banded bats went unrecorded for a year or more and some died before the next opportunity for recapture arose. The recapture histories of most cohorts were brief because of unexpected extermination or because they were banded only a few years before termination of the study. Data from such cohorts give underestimates of survival rates. Each additional sample within a year and each additional year sampled increased the probability of recapturing previously undetected cohort members, partially off-setting the downward bias of the sampling techniques. Thus the cohorts providing the best estimates of survival were those with long histories of concentrated recapture effort. As some banded bats may have lived undetected, even the best estimates should be considered minimal values.

Recapture histories from 1953 to October 1969 of 664 banded cohorts, 386 from summer and 278 from winter, were analyzed to determine yearly survival rate. The cohorts were divided

TABLE 9

CHARACTERISTICS OF COHORTS FROM WHICH SURVIVAL VALUES WERE SELECTED.

Cohort type	Numbers of populations with selected values	Number of cohorts selected	Cohort sample size		
			Total	Mean	Range
		Winter			
Unaged female	2	6	858	143	31–497
Unaged male	2	6	1747	291	100–1088
		Summer			
Unaged female	13	32	12,800	400	29–1416
Unaged male	13	31	4419	143	21–623
Adult female	11	18	2238	124	15–335
Adult male	5	9	257	29	12–54
Immature female	9	11	1048	95	17–217
Immature male	8	10	770	77	20–151

TABLE 10

LIFE TABLE FOR WINTER-BANDED COHORTS OF FEMALE *M. lucifugus*.

x Age interval in years	l_x Number alive at beginning of year interval	d_x Number dying during year interval	q_x Mortality rate of those alive at beginning of interval	e_x Mean life left to those reaching interval
0.5–1.5	1000	687	0.687	2.32
1.5–2.5	313	45	0.143	5.31
2.5–3.5	269	38	0.143	5.11
3.5–4.5	230	33	0.143	4.88
4.5–5.5	197	28	0.143	4.61
5.5–6.5	169	24	0.143	4.29
6.5–7.5	145	21	0.143	3.92
7.5–8.5	124	18	0.143	3.49
8.5–9.5	107	15	0.143	2.99
9.5–10.5	91	13	0.143	2.41
10.5–11.5	78	11	0.143	1.72
11.5–12.5	67	10	0.143	0.93
12.5–13.5	58	–	–	–

TABLE 11

LIFE TABLE FOR WINTER-BANDED COHORTS OF MALE *M. lucifugus*.

x Age interval in years	l_x Number alive at beginning of year interval	d_x Number dying during year interval	q_x Mortality rate of those alive at beginning of interval	e_x Mean life left to those reaching interval
0.5–1.5	1000	635	0.635	1.96
1.5–2.5	365	84	0.229	3.49
2.5–3.5	282	64	0.229	3.38
3.5–4.5	217	50	0.229	3.24
4.5–5.5	167	38	0.229	3.05
5.5–6.5	129	30	0.229	2.81
6.5–7.5	99	23	0.229	2.50
7.5–8.5	77	18	0.229	2.09
8.5–9.5	59	14	0.229	1.57
9.5–10.5	46	10	0.229	0.89
10.5–11.5	35	–	–	–

TABLE 12

LIFE TABLE FOR SUMMER-BANDED COHORTS OF UNAGED FEMALE *M. lucifugus*.

x Age interval in years	l_x Number alive at beginning of year interval	d_x Number dying during year interval	q_x Mortality rate of those alive at beginning of interval	e_x Mean life left to those reaching interval
0–1	1000	528	0.528	2.15
1–2	472	134	0.283	2.99
2–3	338	96	0.283	2.98
3–4	243	69	0.283	2.95
4–5	174	49	0.283	2.92
5–6	125	35	0.283	2.88
6–7	89	25	0.283	2.82
7–8	64	18	0.283	2.74
8–9	46	13	0.283	2.62
9–10	33	9	0.283	2.46
10–11	24	7	0.283	2.23
11–12	17	–	–	–

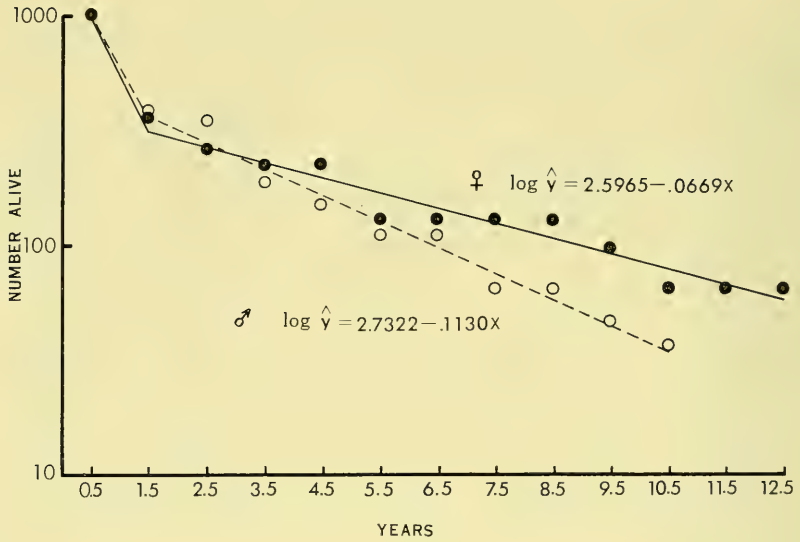

FIG. 19. Survival of unaged *M. lucifugus* banded in winter.

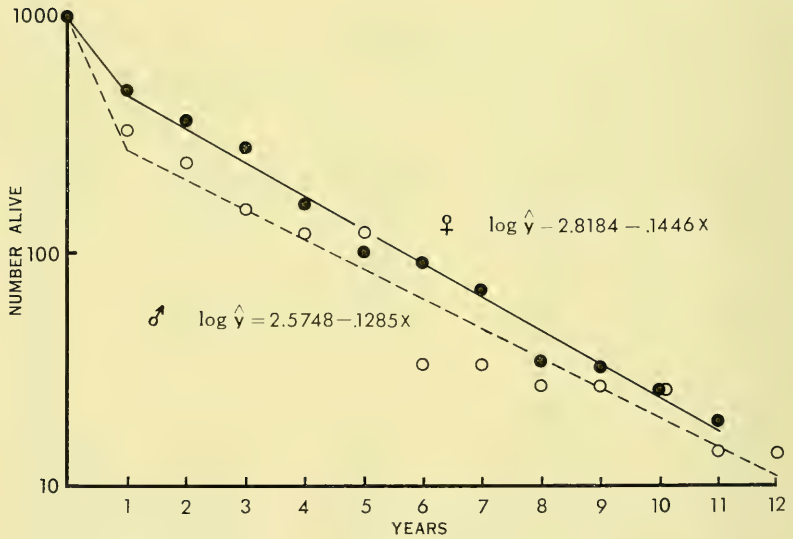

FIG. 20. Survival of unaged *M. lucifugus* banded at nurseries.

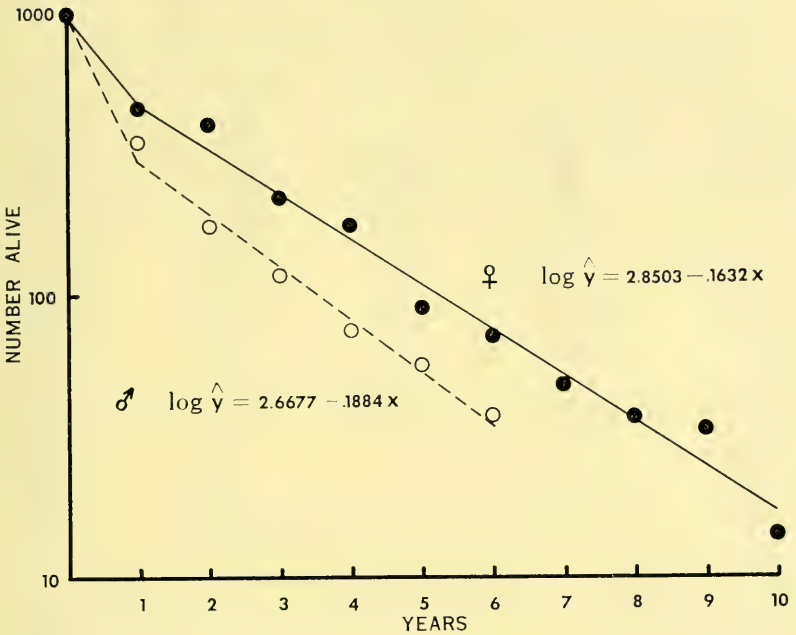

FIG. 21. Survival of adult *M. lucifugus* banded at nurseries.

into eight groups according to age, sex, and season of banding. Sample characteristics of these cohorts are given in Table 9. Because no population was sampled every year, data from all cohorts underestimated actual survival. To characterize survival patterns it was necessary to select the highest value for the xth year within each type of cohort. Each of these values was supported by several slightly lower values from other cohorts, suggesting that the selected values were typical rather than abnormally high. A composite set of highest minimal values was then plotted for each type of cohort.

Semilogarithmic plots of percentage survival values (Figs. 19–22) were examined for constant rates of change. For each type of cohort the survival rate for the first year was much lower than for subsequent years. For the remaining portions of the curves no nonlinear patterns were evident, so the minimum survival rates were asumed to be constant after one year of age (one to n years on each curve). The specific rate for each curve was

TABLE 13

LIFE TABLE FOR SUMMER-BANDED COHORTS OF UNAGED MALE *M. lucifugus*.

x Age interval in years	l_x Number alive at beginning of year interval	d_x Number dying during year interval	q_x Mortality rate of those alive at beginning of interval	e_x Mean life left to those reaching interval
0–1	1000	720	0.720	1.55
1–2	280	72	0.256	3.27
2–3	208	53	0.256	3.23
3–4	155	40	0.256	3.17
4–5	115	29	0.256	3.08
5–6	86	22	0.256	2.98
6–7	64	16	0.256	2.83
7–8	47	12	0.256	2.63
8–9	35	9	0.256	2.36
9–10	26	7	0.256	2.00
10–11	19	5	0.256	1.52
11–12	14	4	0.256	0.87
12–13	11	–	–	–

approximated with a linear regression line. Because survival rates of individual cohorts were used rather than the less realistic mean rates, no probability statements may be made about the resultant regression equations. These data do not support statistical tests of the constancy of survival rates within a cohort type or of the equality of the survival rates of different cohort types.

Life tables (Tables 10–17) were calculated following the example of Deevey (1947). Estimates of the number per thousand alive at the beginning of each year-interval were obtained from the regression equations. Use of the actual values for this purpose would be misleading because in some years values were no higher than in the following year, an artifact of sampling schedules giving the appearance of 100 per cent survival.

The low survival in the first year compared to later intervals is not surprising in immature and unaged samples (which include some immatures). Such a pattern is typical of young mammals (Caughley, 1966). However, the low first year survival of adult samples was not expected, because the second and subsequent years of immature samples show constant rates

TABLE 14

LIFE TABLE FOR SUMMER-BANDED COHORTS OF ADULT FEMALE *M. lucifugus*.

x Age interval in years	l_x Number alive at beginning of year interval	d_x Number dying during year interval	q_x Mortality rate of those alive at beginning of interval	e_x Mean life left to those reaching interval
0–1	1000	513	0.513	2.01
1–2	487	152	0.313	2.60
2–3	334	105	0.313	2.56
3–4	229	72	0.313	2.50
4–5	158	49	0.313	2.41
5–6	108	34	0.313	2.28
6–7	74	23	0.313	2.09
7–8	51	16	0.313	1.82
8–9	35	11	0.313	1.42
9–10	24	8	0.313	0.84
10–11	17	–	–	–

of survival. This suggests that some individuals responded to our banding procedure in a manner that actually or apparently reduced survival during the first year. A few loosely applied bands are undoubtedly lost, but this probably does not account for all of the difference. Until learning how to maneuver with a band, bats also may be subject to increased mortality from accidental collisions or snagging in the air or roost. Several banded animals died from exposure after snagging their bands in a crack at an exit of the Pennville nursery. The possibility that some individuals move permanently to other sites is not supported by movement data.

Because immature cohorts best represent the full life history of *M. lucifugus*, they should be more useful than the other cohorts in explaining demographic behavior of these populations. Unfortunately the immature cohorts and, to a lesser extent, those of adults had brief recapture histories and thus gave underestimates of survival. A further difficulty is that mortality of immatures in their first month of life is not accounted for, as only volant bats were banded. The unaged cohorts banded at nurseries and caves had long recapture histories. If no factor other than mortality affected survival estimates, the first-year survival ($1–q_x$ in Tables 10–17, or slopes

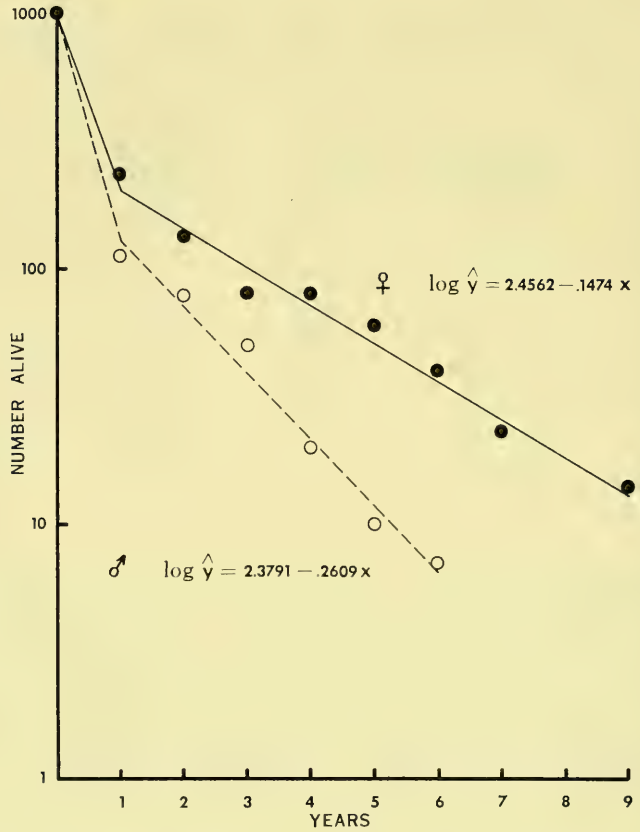

FIG. 22. Survival of immature *M. lucifugus* banded at nurseries.

of lines in Figs. 19–22) in nursery-banded cohorts should be relatively high for adults, low for immatures, and intermediate for unaged animals. Among females, survival rates of adults and unaged bats are approximately equal and much higher than that of immatures. The much longer recapture histories of unaged cohorts increase apparent survival, compensating for the inclusion of immature animals. For males, survival in unaged cohorts should be almost as low as immature survival because most unaged males in nurseries were immature. Instead, survival of unaged bats is almost as high as that of adults, whereas immature survival is much lower. The difference in survival

TABLE 15

LIFE TABLE FOR SUMMER-BANDED COHORTS OF ADULT MALE *M. lucifugus*.

x Age interval in years	l_x Number alive at beginning of year interval	d_x Number dying during year interval	q_x Mortality rate of those alive at beginning of interval	e_x Mean life left to those reaching interval
0–1	1000	698	0.698	1.34
1–2	302	106	0.352	2.29
2–3	195	69	0.352	2.27
3–4	127	45	0.352	2.23
4–5	82	29	0.352	2.17
5–6	53	19	0.352	2.07
6–7	34	–	–	–

between unaged and immature males probably is due to differences in their respective recapture histories. Perhaps the first-year survival of immature males is actually only slightly less than adult male survival.

If, again, mortality is the only factor operating, the survival curves of nursery-banded adults, immatures, and unaged bats should have equal slopes for the second and subsequent years, when all individuals are adult. Among females, unaged and immature cohorts have almost identical slopes and adult cohorts have slightly lower survival, having shorter recapture

TABLE 16

LIFE TABLE FOR SUMMER-BANDED COHORTS OF IMMATURE FEMALE *M. lucifugus*.

x Age interval in years	l_x Number alive at beginning of year interval	d_x Number dying during year interval	q_x Mortality rate of those alive at beginning of interval	e_x Mean life left to those reaching interval
0–1	1000	796	0.796	1.17
1–2	204	59	0.288	2.78
2–3	145	42	0.288	2.70
3–4	103	30	0.288	2.59
4–5	74	21	0.288	2.43
5–6	52	15	0.288	2.21
6–7	37	11	0.288	1.90
7–8	26	–	–	–

TABLE 17

LIFE TABLE FOR SUMMER-BANDED COHORTS OF IMMATURE MALE *M. lucifugus*.

x Age interval in years	l_x Number alive at beginning of year interval	d_x Number dying during year interval	q_x Mortality rate of those alive at beginning of interval	e_x Mean life left to those reaching interval
0–1	1000	869	0.869	0.78
1–2	131	59	0.452	1.67
2–3	72	33	0.452	1.63
3–4	39	18	0.452	1.56
4–5	22	10	0.452	1.43
5–6	12	5	0.452	1.20
6–7	7	–	–	–

histories than unaged groups and less frequent recapture attempts than immature groups. Among males, unaged cohorts exhibited substantially higher survival than adult cohorts, which in turn showed higher survival than immature groups. This pattern is related directly to shorter recapture histories and less intensive sampling effort, so the unaged estimate is probably most realistic. Winter-banded cohorts have the longest recapture histories and most consistent sampling effort and thus should provide the best estimates of survival. Although within-winter changes in population size confound survival data, we may have avoided the effects of behavioral changes by taking most samples in late winter when populations were large. At the time of banding, winter cohorts included unknown numbers of immatures.

Based on the above considerations, Table 18 presents the best estimates of *M. lucifugus* survival available for this study. Some of the values are in agreement but others that theoretically should be similar are not. Whether the constant rate of survival after the first year is real or an artifact of the smoothing procedure used is a vital question. Caughley (1966) reviewed mammalian survival patterns and found that the post-juvenile phase may exhibit either a constant rate or a steadily decreasing rate of survival. The pattern found in the present study needs verification by studies in which recapture effort can be quantified.

From the best estimates we conclude that mean life expec-

TABLE 18

ESTIMATES OF PERCENTAGE ANNUAL SURVIVAL OF *M. lucifugus*.

Cohort type	First year	Subsequent years
Immature female	$20.4 \leq ? \leq 47.2$	71.2
Adult female	48.7	71.7
Winter female	31.3	85.7
Immature male	27.9	74.4
Adult male	30.2	74.4
Winter male	36.5	77.1

tancy (e_x for year interval 0–1) is 1.55 years for males and from 1.17 to 2.15 years for females. For the reasons given above we think that the correct figure for females is actually slightly greater than two years.

The maximum longevity recorded in this study was 14 years for a nursery-banded female. Longevities of 20.5 years (Hall *et al.,* 1957; Hitchcock, 1965) and 24 years (Griffin and Hitchcock, 1965) have been reported from the northeastern United States.

Natural Causes of Mortality

The single most important nonhuman cause of *M. lucifugus* mortality is probably accidents encountered while flying or seeking shelter. The variety of such accidents is well illustrated by the circumstances accompanying recapture of 172 bats by citizens. Of the total, 17 per cent were found dead, 14 per cent were killed when captured, 9 per cent were released alive, and the disposition of the remaining 59 per cent was not specified. Most of these animals were taken in or near human dwellings or utility buildings. Most of the dead bats were found in spring and autumn, many during cold weather or after cold nights. Some of the bats killed when captured were reported as appearing sick or injured. The number of recaptures did not vary strongly by season, although there were somewhat fewer reports from summer (17.4 per cent), when females were in nurseries. The 65 recaptures of nursery-banded bats provided particularly interesting information because almost all (97.1 per cent of 9462) males banded were immatures. In contrast to females (28,516

banded), males comprised a significantly higher proportion of the bats reported than of those banded ($X^2 = 45.124$, $P < 0.005$). On a seasonal basis, the differences in proportions were greatest in summer, autumn, and winter. Thus it appears that mortality of immature males was significantly higher than mortality of unaged females (banded in proportions of approximately two adults to one immature) during their first summer, autumn, and winter, but was not different in their first spring. We have no records of large numbers of deaths during autumn migration as reported by Zimmerman (1937), but do not doubt that similar mishaps frequently befall individuals or small groups of bats. This species sometimes dies in the warm months by becoming snagged on sharp objects such as burdock seeds (*Arctium minus*) (Lyon, 1925). Cave-banded bats showed no significant disproportions between numbers banded and recaptured by citizens. Both sexes at caves included immatures and adults, and by winter much of the high immature male mortality had already occurred.

When individuals of *M. lucifugus* are highly clumped in roosts they are vulnerable to drastic reduction or extermination by natural catastrophes. This is especially critical at nurseries. However, in this study nonhuman agents of mortality were not important at nurseries. Every nursery contained a few dead immatures and adults but the number was always small. Large scavengers did not enter nursery roosts and remove bat carcasses. Predation was observed at only one nursery. House cats occasionally stood on the roof of the Pennville nursery at twilight and tried to catch flying bats. Children found eight partly eaten bats or bands in the gravel driveway next to the house in 1964 and 1965. The eaves of the Thorntown nursery housed a nesting pair of sparrow hawks, but their activity period did not overlap that of the bats. The only observation of attack by predatory birds was the capture of two *M. lucifugus* by a screech owl during a nursery exit flight. Once during a flight count we observed a great blue heron attempt to catch a hoary bat, *Lasiurus cinereus*, in the air; however, no such attacks on the more numerous *M. lucifugus* were observed. Smith (1954) also noted low mortality at *M. lucifugus* nurseries.

A number of mortality agents operate in caves, but there is no compelling evidence that these often are important. DeBlase

et al. (1965) reported the death of approximately 2850 *M. lucifugus,* virtually an entire winter population, when Wind Cave flooded in March 1964. This is the only such catastrophe known for this species and is surely a rare event. Miscellaneous reports of predators on this species in caves include house cats (Blatchley, 1896), voles (Martin, 1961), mice (Hitchcock, 1965; Fenton, 1970), and a pine martin (Fenton, 1970). Only one definite case of predation in a cave was found in the present study. At Wyandotte Cave in the autumn swarming period of 1968 a house cat caught several bats that were flying through a low passage of the cave entrance. We commonly observed tracks of raccoons and mink in Indiana and Kentucky caves but concluded that their prey only occasionally included bats that had fallen to the floor. *M. lucifugus* rarely chooses roost sites within reach of such predators. Davis and Hitchcock (1965) found that many young *M. lucifugus* entered hibernation without storing large amounts of fat and postulated that these fail to survive the winter. We also observed numerous thin bats in late autumn and early winter. Even considering the irregular visits of scavengers that remove bat carcasses from the cave floor, we so seldom saw dead bats on the floor or in roost cracks that without further evidence we are not prepared to accept this as a probable cause of significant mortality in our study area.

Three citizen recaptures away from caves in winter demonstrate that some mortality occurs when bats move about during cold weather. A female from the Shoals nursery was recaptured in a house 14 km. S Shoals on 15 December. A male from the Franklin nursery was found dead behind a house screen door on 13 January in Milltown, Crawford Co., Indiana. A female netted at Wyandotte Cave on 29 August 1963 was found dead, clinging to the south side of a house 13 km. W Columbus, Bartholomew Co., Indiana, on 20 December 1963. The temperature was below freezing at the time.

Human-Related Population Declines

Humphrey (1964) commented on destruction of *M. lucifugus* nurseries in Indiana, and Cope and Hendricks (1970) presented a more recent account. This and other information is included in Table 19. The population size values are approximate and,

TABLE 19

CHANGES IN *M. lucifugus* NURSERY POPULATION SIZE (ADULT FEMALES AND YOUNG) IN RELATION TO DESTRUCTIVE ACTIVITY.

Nursery	Population estimate early in study	Year of known destructive activity	Population estimate after activity	Year of most recent population estimate
Benton	140	none	140	1969
Brookville	650	1968	0	1969
Camden	200	none	200	1962
Carthage	400	none	400	1964
Cicero	200	none	200	1964
Cortland	350	none	350	1964
Etna	300	1968	300	1969
Franklin	600	1964	250	1964
Macy	200	none	200	1969
Milroy-East	170	none	170	1960
Milroy-South	800	1968, 1969	275	1969
New Castle	600	unknown	35	1969
Newbern	850	1968	0	1969
Pennville	1360	1969	580	1969
Pine Village	110	none	110	1966
Pittsburg	220	none	220	1962
Reelsville	1200	1968	0	1969
Rushville	100	none	100	1968
Shirley	600	1964	30	1964
Shoals	3000	1963, 1969	875	1969
Thorntown	700	1969	250	1969
Tunnelton	1800	none	1800	1969
Williamsburg	900	none	900	1969
Total	15,450		7385	

except for Pennville and Thorntown, are based on visual estimates. Because most estimates were made later in the autumn than the July peak documented by flight counts at Pennville and Thorntown, it is probable that most estimates were of populations already reduced by migration. Thus it can be assumed that these are underestimates in most cases. The "early estimate" column total provides a conservative estimate of the number of *M. lucifugus* accounted for in the Indiana nurseries we selected for detailed study, namely 15,450 adult females and their young.

Destructive activity in nurseries varied in type and impact. The Brookville colony was exterminated by application of DDT dust to the bats and roost surfaces. Bats failed to reoccupy the Newbern nursery after naphthalene mothballs were hung in the roost sites in the spring. At Shoals, where the population inhabited four buildings, bats in one building were poisoned in 1963 and their access holes were caulked in 1964. Another Shoals roost was partially exterminated in 1969 with DDT dust and automobile exhaust. Reroofing of the Reelsville roost excluded bats. Thirty *M. lucifugus* remained in the Shirley nursery a month after it was reroofed in mid-summer. A month after reroofing of the Franklin attic, about 250 bats were found in a nearby barn and fewer than 10 in the house. The owner of the Etna house caulked access holes and killed many bats inside the attic with a tennis racket, but some holes and bats remained. No decrease is recorded in this case because the early estimate was taken well after autumn migration had begun. The Pennville population was reduced 48 per cent when examined in 1969, apparently because a door in the attic wall had fallen in, increasing the amount of light and air circulation in the roost. This probably limited the area of suitable microclimate to the deepest recesses of the attic. The house was reroofed in 1970 but a reduced population continued to inhabit the attic. A similar change in microclimate occurred at Thorntown when vandals broke holes in the roof of the abandoned house. The Milroy-South nursery declined from 800 to about 275 adult females and young, primarily because in 1968 and 1969 many bats, including our banded individuals, were collected. We cannot explain the fairly regular decline at the New Castle colony from 600 in 1958 to 400 in 1965 and 35 in 1969.

We learned of the loss of three other Indiana *M. lucifugus* nurseries when exterminators reported banded bats. In 1964 a man near Tipton, Tipton County, exterminated a colony in his attic by spraying the bats and their roost with DDT solution. This was apparently a medium-sized population. A nursery of 1500 adult females and young in Columbus, Bartholomew County, and one of unknown size in Vallonia, Jackson County, were destroyed by professional exterminators in 1963 and 1965, respectively. Aside from documenting additional losses, these

records confirm the likelihood that some nurseries were not detected during our study.

Recapture records document the fate of a few bats whose nurseries were destroyed. One bat was recaptured after the poisoning at Brookville. A female banded there on 23 August 1960 was found 19 kilometers north at a nursery in Dunlapsville, Union County, Indiana, on 13 August 1970. The only Newbern bat taken after repellant application in 1968 was a female (banded on 28 July 1958) found in the Tunnelton nursery on 14 August 1969. None of the Shirley bats was recaptured after the post-roofing check in August 1964, when 30 were still present. Within a few days of reroofing at Reelsville in 1968, two females banded on 12 August 1960 and 13 July 1965 were captured while trying to find shelter in separate (unsuitable) buildings in Reelsville. A female banded at Reelsville on 12 August 1960 was taken 6 kilometers away near Lena, Parke County, on 14 May 1969. One Franklin female, banded on 30 July 1959, was taken in the Thorntown nursery on 14 August 1964, four days after the post-roofing check. A male banded during this visit was captured behind a screen door in Milltown, Crawford Co., Indiana, on 13 January 1967. No bats from these five nurseries were recaptured in hibernacula following nursery destruction. A survey of all buildings within a radius of two kilometers from the Thorntown nursery during extensive sampling disturbance in the summer of 1964 revealed no movement other than to the other roost of the two-building colony. Clearly individuals sought suitable alternate roost sites after exclusion, but there is no evidence of successful or even attempted group establishment at a new roost. Perhaps a few females (each several years old) relocated in previously established nurseries. Thus virtually all bats eliminated from an established colony site seem to disappear.

The summed population estimates before and after destructive activity at nurseries show a drop from 15,450 adult females and young to 7385, a 52.2 per cent decline in about a decade. Further, eight of the 23 populations have not been examined since 1964 or earlier, and it is probable that some of these have been destroyed as well.

In Ray's Cave we noted occasional losses of hibernating bats to

TABLE 20

SIZE ESTIMATES OF *M. lucifugus* POPULATIONS IN SELECTED HIBERNACULA.

Year	Ray's Cave	Grotto Cave	Wind Cave	Wyandotte Cave	Coon's Cave
1960–61	–	2000	–	–	900
1961–62	2680	1525	–	350	–
1962–63	25	–	7000	175	–
1963–64	1800	–	2850	150	225
1964–65	5600	1377	–	900	–
1965–66	1300	–	116	500	350
1966–67	1800	1180	200	550	–
1967–68	70	–	130	140	–
1968–69	350	190	162	24	–
1969–70	575	266	84	4	–

human activity, once when vandals killed about 100 *M. lucifugus* and *M. sodalis* with torches and several times when bats were collected for laboratory experiments. Hitchcock (1965) recorded loss of *M. lucifugus* to collectors, and Fenton (1970) noted several cases of extensive mortality resulting from commercial enterprises in caves.

Estimates of hibernating populations of *M. lucifugus* show a strong downward trend over a 10-year period (Table 20). Because much variation resulted from not using a standard census date, the largest value is given when more than one estimate was made in a particular winter. The low estimate of 25 bats at Ray's Cave in 1962–63 was made in November without a later check for increased numbers. The Wind Cave flood (DeBlase *et al.*, 1965) occurred shortly after the estimate of 2850 was made, accounting at least in large part for subsequent low estimates there. The most marked and synchronous decline occurred between the winters of 1966–67 and 1967–68.

Several factors may be involved in this decline. One significant cause is the extermination of nursery populations or destruction of roost structures. Unfortunately we do not know what proportion of the winter population is represented by the nurseries that we monitored. Another factor may be hibernaculum disturbance by spelunkers and researchers, which may have caused many bats to seek less disturbed caves or retreat to places where people cannot go. Some species are quite sensi-

tive to such disturbance (for example, *Myotis grisescens*—M. D. Tuttle, personal communication; *Myotis velifer*—Tinkle and Patterson, 1965, T. H. Kunz, personal communication, Humphrey, unpublished data; *Eptesicus fuscus*—Beer, 1955, Hitchcock, 1965, Phillips, 1966). However, there are no data suggesting that *M. lucifugus* avoids disturbed hibernacula. Hitchcock (1965) visited two fairly large hibernacula almost annually for 23 years and found no decline in *M. lucifugus* populations, whereas a marked decline in numbers of *E. fuscus* occurred. In the present study a few *M. lucifugus* moved from one cave to another, up to 16 kilometers away, within a winter. Several banded in one cave in winter hibernated in a different cave during a subsequent winter. This suggests that some disturbed bats will move to other caves, but probably not enough bats are involved to account for the observed declines. A third possible cause, which has not been investigated for this species, is accumulation of lethal amounts of pesticides. High levels of DDT and DDE have been implicated in a severe decline of a Mexican free-tailed bat (*Tadarida brasiliensis*) population in Arizona (Cockrum, 1970). The suggestion of a threshold effect in the fairly distinct decline in *M. lucifugus* populations between the winters of 1966–67 and 1967–68 (Table 20) lends credence to this hypothesis, particularly as this time period does not correspond with the years in which nursery destruction occurred (Table 19).

ECOLOGICAL STRATEGIES

Like other species of insectivorous bats living in temperate climates, the little brown bat has a food supply available only part of the year. Species attempting to fill such a niche are subject to severe constraints. *M. lucifugus* has adapted to these conditions by being energetically conservative and performing all species-maintenance functions during the warm months.

Perhaps the principal adaptive strategy of *M. lucifugus* is a pattern of thermoregulation shared, at least in general characteristics, with other temperate species of insectivorous bats (Lyman, 1970). During the cold months and when at rest in the daytime during the warm months, body temperature drops to within a degree of the ambient temperature. This allows a reduction of metabolic rate and thus of the amount of food required. Energy stored in adipose tissue is used during extended winter hibernation. It is noteworthy that an individual *M. lucifugus* possibly may spend the majority of its lifetime in torpor.

The proper functioning of this thermoregulation strategy requires an optimal thermal environment in the roost. *M. lucifugus* thus appears to have rather specific roost microclimate requirements, and availability of suitable roosts is probably a limiting factor. A hibernaculum must have a stable, cool temperature, high humidity, and low air flow rates that minimize evaporative water loss. Such sites are apparently found only in natural or artificial caves. A nursery must be thermally stable with temperatures in the thermal neutral zone of the species (39 to 42° C according to Stones and Wiebers, 1965). Temperatures in this zone permit daily torpor in adults and promote rapid growth of the young, which are poor thermoregulators. Suitable nursery sites are apparently usually found only in tree recesses and man-made structures and only rarely in caves.

The scarcity of roost sites with optimal microclimatic qualities leads to strong clumping of individuals. As a result, *M. lucifugus* occurs in fairly large populations of one sort or another throughout the year. Winter populations are restricted to areas

where caves and mines occur. Summer populations are much more widely distributed, including but extending well beyond cave and mine regions. Bats are in both types of roosts in spring and autumn. It is not clear whether this species uses cumulative body heat to warm the air in nursery roosts as some cave-dwelling species do, or whether nursery microclimate is too variable for such control to be applied.

Food gathering is a species maintenance function that has been little studied in *M. lucifugus* (Gould, 1955). Aside from the obvious importance of acquiring energy for individual metabolism, production of young, and accumulation of fat, future studies of food habits may help answer questions on limiting factors, the relation of food supply to nurseries, and the distinctness of populations in nearby nurseries. Do individuals compete for food or are enough insects available even in cool weather to justify the expenditure of foraging energy regardless of population density? Competition for food (or roost space) could explain why newly established populations become stable rather than continuing to increase. Competition could share the influence of roost site scarcity on the lack of summer inter-colony movement and on the high degree of natal site attachment exhibited by females. Competition also could be responsible, along with roost site scarcity, for the wide dispersal of *M. lucifugus* in summer colonies.

The distribution of populations shown in Fig. 1 is no doubt greatly biased by our searching procedures. A more realistic view of the total yearly distribution of the animals we studied is given by citizen reports (Fig. 23). The functional unit whose distribution is outlined can be considered a deme, a distinct population of interbreeding animals. Existence of demes is apparently quite common in temperate zone bats, although they have not been clearly identified as such. Roer (1960) concluded that two distinct populations of *Myotis myotis* exist in northern Europe, and Hall (1962) stated that *Myotis sodalis* have "populational ranges" that restrict gene flow. Hall and Wilson (1966) discussed a large "populational home range" of *Myotis grisescens.* Deme distribution is probably equivalent to the "familiar area" recognized by Davis (1966). Dwyer (1966) described for *Miniopterus schreibersii* three "partially discrete breeding populations,

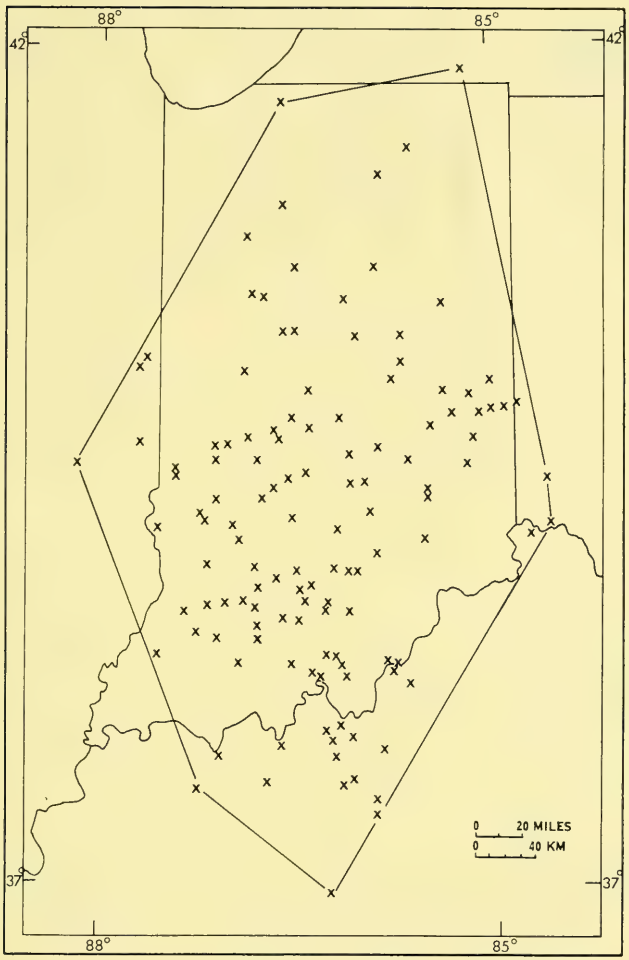

FIG. 23. Distribution of the Indiana *M. lucifugus* deme based on citizen recaptures of banded animals.

occupying specific population ranges . . . within which gene flow would be at a high level but between which gene flow would be more or less restricted." Dwyer (1969) suggested that such populations "may approach deme status." Cockrum (1969), in reviewing data on migration of *Tadarida brasiliensis,* concluded that "four or more behaviorally (and possibly genetically) sepa-

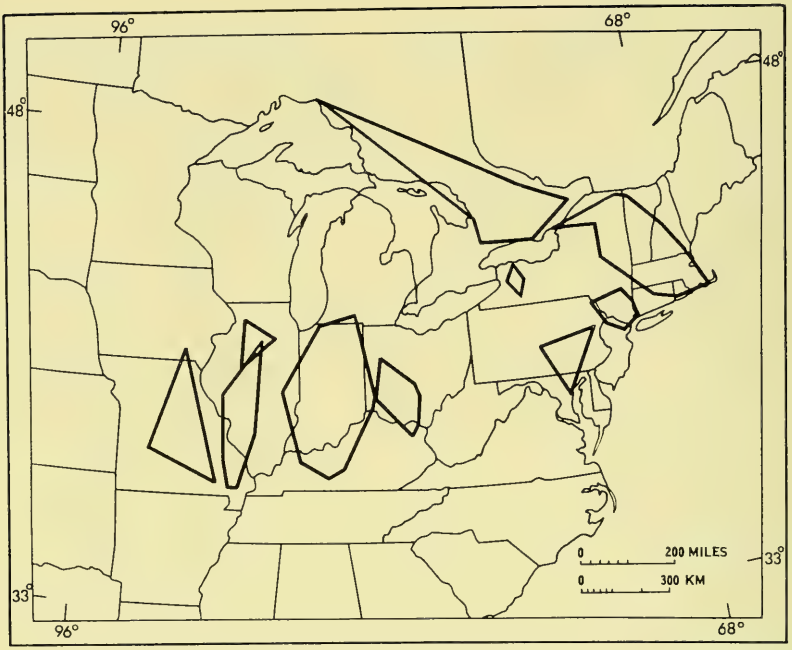

FIG. 24. Distribution of *M. lucifugus* demes in eastern North America based on published information. Data are from Barbour and Davis (1969); Carmody *et al.* (1971); Davis and Hitchcock (1965); Fenton (1970); Griffin (1940*a*, 1945); Hall and Brenner (1968); Humphrey and Cope (1964); Layne (unpublished); Mills (unpublished); Myers (1964); Walley (1971); and this study.

rate populations" exist in the western United States. Barbour and Davis (1969) illustrated distributions of what appear to be two demes of *Myotis sodalis*. Much of the eastern subspecies of *M. lucifugus* seems to be organized into demes. The approximate distribution of these demes is shown in Fig. 24.

These deme ranges will become more clearly defined as recapture data accumulate. Ascertaining the degree of overlap or distinctness will clarify patterns of gene flow. Movement data from bats banded at boundaries between demes would be especially instructive. In our study, only two foreign recaptures occurred beyond the boundaries shown in Fig. 23. A female banded at Grotto Cave on 8 February 1964 was found dead on 26 June 1966 in Chandlerville, Cass Co., Illinois, 319 kilometers

to the west-northwest. Another female banded at Grotto Cave on 21 February 1965 was recaptured on 2 August 1966 at Merton, Waukesha Co., Wisconsin, 465 kilometers to the north-northwest. Of thousands banded in another deme in north-central Illinois, H. D. Walley (personal communication) has recorded only one case of overlap, an individual recaptured in the autumn in Indianapolis, Marion Co., Indiana. These records could be discarded because of possible errors in band-reading. On the other hand, these movements are no longer than our longest migratory records, simply in the wrong direction. Fenton's (1969*b*) long-distance records for the species based on confirmed band-readings far exceed ours. Perhaps our anomalous records are of bats that became disoriented during migration. Such wanderers probably account for little gene flow between demes. Probably most of the extralimital records of *M. lucifugus* summarized by Barbour and Davis (1969) also represent disoriented individuals, as all are within normal movement distance of areas with established populations. Overlap of the groups in western and northern Illinois as drawn in Fig. 24 is based on a single movement. The lack of interchange despite concurrent banding and recapturing of many thousands of *M. lucifugus* by R. S. Mills in southwestern Ohio, W. H. Davis in eastern and southern Kentucky, H. D. Walley in northern Illinois, and R. F. Myers in Missouri and western Illinois, constitute substantial negative evidence in favor of our deme hypothesis.

Although the Indiana group of *M. lucifugus* is rather distinctly isolated from others, justification of the claim of deme status demands consideration of the functional properties of such a geographical unit. Probably the most important functions of the unit relate to fall movement and in particular to swarming. Davis and Hitchcock (1965) and Fenton (1969*b*) suggested that autumn swarming functions in the selection of a winter roost site. Our data neither support nor refute this hypothesis. Autumn swarming may be an important aspect of gene flow. Swarming is a behavior by which *M. lucifugus* (and probably other species), dispersed over a wide geographical area in nurseries and male roosts, come together to breed. This prevents both failure to find a mate and the local inbreeding that would occur if a nursery population was its own gene pool.

Thus, the origin of the Indiana-Kentucky deme must relate to the restricted distribution of swarming sites in relation to suitable summer roosts. Where swarming sites are more uniformly distributed than in our study area the existence of demes may be less likely.

Swarming probably does not produce a completely homogeneous mixture of breeding animals, judging from the lack of inter-cave movement in autumn and the differences in fall visitation of Wyandotte as opposed to Wind and Dixon caves. Further development of this thesis depends on better information regarding the relative importance of nurseries, swarming sites, and hibernacula as centers for copulation. Detailed behavioral observations at these locations in autumn, winter, and spring would provide insight into the uniformity or routes of gene flow within a deme.

Based on current information, we believe that gene flow between *M. lucifugus* demes could be low enough to promote genetic divergence. Examination of morphological and physiological characteristics might reveal variation between demes. In comparison to the eastern half of the range of the species, the steeper environmental gradients and stronger discontinuities of habitats encountered by this species in western North America may be expected to exert stronger selective pressures. Perhaps the deme-swarming pattern found in the eastern subspecies also occurs in western populations and functioned as an isolation mechanism in the separation of *M. l. occultus* from *M. l. carissima.*

Future studies of swarming should consider the possibility, inferred here from secondary dispersal records and population differences in adult and unaged sex ratios, that the familiar area of the average male *M. lucifugus* may be more closely confined to the cave region than that of the average female.

Because patterns of hibernaculum use also may relate to gene flow, movements from nurseries to winter roosts may reveal regional subunits of the deme. Our data (Figs. 2–7) show that nursery populations differ in the extent to which they use a given cave in the winter. Evaluation of these data (Table 21) indicates a spectrum of differential movement from nurseries in various parts of the deme. Populations in several areas behaved similarly; three groups of such populations were recognizable.

TABLE 21

RELATIVE REGIONAL MOVEMENT OF *M. lucifugus* FROM NURSERIES TO HIBERNACULA, INCLUDING MOVEMENTS OF BOTH SEXES FROM SUMMER OR AUTUMN TO ANY WINTER.

Nursery of origin	Number of recaptures	Per cent recaptures in each cave region				
		Ray's[1]	Donnehue's[2]	Wyandotte[3]	Wind	Mammoth[4]
Northwestern[5]	70	81	1	4	6	7
Reelsville	84	96	1	2	0	0
Shoals	61	61	5	10	3	21
Tunnelton	38	24	21	24	21	11
South-central[6]	44	5	2	5	23	66
East-central[7]	23	35	9	13	22	48

[1] Ray's, Grotto, Coon's, Brinegar's, Buckner's, Shaft, Salamander, and Sullivan's caves.
[2] Donnehue's, Blue Spring, Bronson, Donaldson's, Endless, and Nymon caves.
[3] Wyandotte, Saltpeter, and Parker's Pit caves.
[4] Dixon, Colossal, Mammoth, Long's, Short, and Coach-James caves.
[5] Benton, Etna, Macy, Camden, Pittsburg, Pine Village, Cicero, and Thorntown.
[6] Franklin, Newbern, and Cortland.
[7] Shirley, New Castle, Williamsburg, Brookville, and Milroy-South.

Bats from the northwestern nurseries and Reelsville almost all moved to the northernmost caves. Shoals bats concentrated there also but showed more movement to caves farther south. Tunnelton bats moved almost uniformly throughout the cave region. Bats from the south-central nurseries almost all moved to the southernmost caves, whereas bats from east-central nurseries concentrated at both southernmost and northernmost caves. These differences may reflect partial routes of gene flow within the deme.

The differences in movement patterns also provide clues regarding possible modes of long-distance orientation in *M. lucifugus*. Data and speculation in the literature on numerous bat species indicate (1) that bats migrate in groups (for example, unknown species, Hammond, 1948, and *Tadarida brasiliensis*, Constantine, 1967) and (2) that bats move in apparent relation to a variety of physiographic features (see review and supplemental data of Dwyer, 1969, and review by Griffin, 1970). Implicit have been assumptions that many bat species are capable of coordinated group movement (such as in feeding flights of *T. brasiliensis*, Humphrey, 1972) and that they are capable of detecting landmarks from a distance beyond the

range of echolocation. Acceptance of these assumptions may lead to another—that bats learn and remember the topography of a large geographical area. Data on migration in *M. lucifugus* are consistent with these ideas. Zimmerman (1937) showed that this species may move in groups. Our records of large numbers of individuals arriving at, and leaving, nurseries (Fig. 11) and swarming caves (Fig. 13) also suggest coordinated group behavior. The movement patterns in Figs. 2–7 and Table 21 probably reflect response to physiographic features. The movement of south-central and east-central bats to the southernmost caves suggests that bats, perhaps low-flying, do not move over the eastern escarpment of the Norman Upland and Mitchell Plain, which extends from a point between Franklin and Martinsville to New Albany, Indiana. Instead they appear to move down the Scottsburg Lowland and Muscatatuck Regional Slope, across the Ohio River, along the western edge of the flat Outer Blue Grass Region and over The Knobs to the Kentucky caves. (For maps of relief and physiographic regions refer to the *National Atlas of the United States*, 1970, Schneider, 1966, and Lobeck, 1929.) Hall's (1962) view that *Myotis sodalis* migrates by following water bodies does not seem applicable to this *M. lucifugus* deme. It would invoke unnecessarily long and circuitous routes along the Wabash, White, Ohio, and Greene rivers. It would require bats from extreme northwestern Indiana to move west along the Kankakee River, south along the Illinois and Mississippi rivers, and east along the Ohio, whereas bats from the Benton nursery would fly along the St. Joseph River to Lake Michigan. Nonetheless it does seem reasonable to suggest orientation in response to a combination of waterways, escarpments, and other topographic features, perhaps including major highways. Special orientation conditions may exist where *M. lucifugus* is found on the Great Plains, as indicated for northern Illinois by Walley (1971). There the restriction of captures to river valleys also coincides with the distribution of belts of forest, caves, and very old houses.

One of the most important species maintenance functions occurring in nursery populations is reproduction. Although natality data from growing populations are needed for confirmation, it appears that the biotic potential of *M. lucifugus* is one young

per female per year. Apparently this species regularly achieves almost all of its biotic potential. Perhaps environmental conditions in this study were optimal for reproduction.

Data on size of undisturbed nursery populations indicate that populations were stable. Given a stable age distribution, a mean life expectancy of 1.15 years for males allows each male, on the average, to participate in one or two autumn breeding seasons, depending on when it becomes sexually mature. Likewise, a mean life expectancy of slightly more than two years for females means that on the average each female produces two offspring, one female and one male. If the survival data of this study are taken to indicate age distribution (see Table 12), the number of females compared with the number of young they produced during their lifetimes indicates production of only 1.67 offspring per female. This indicates an age distribution more youthful than the stable distribution and shows that our survival values are lower than the real values.

The precise nature of the annual single-birth pulse, consistent achievement of the biotic potential, and strong nursery site attachment leave survival rate as the only labile demographic component available to *M. lucifugus* for increasing population growth. Extremely rapid population growth could not occur because this species has no ability to respond to improved environmental conditions or excessive mortality by increasing natality above the rate recorded here. Instead population growth can begin only by increasing survival rates, and growth would take place relatively slowly as the age distribution became older and females produced a larger number of offspring per lifetime. On the other hand, population declines can result from decreased survival, natality, or site attachment. The fact that growth is not occurring in undisturbed populations that have high natality and site attachment suggests that some density-dependent factor is limiting nursery population size by reducing survival. We have not identified such a factor.

Limiting reproduction to one young a year seems to be a strategy that eliminates the possibility of rapid overpopulation of roosts, while the bats employ changes in survival rates to affect population growth. This solves a potential crowding problem and points to the evolutionary importance of roost site

scarcity as a limiting factor. The single annual birth-pulse has been adopted as a strategy of self-regulation by 12 of the 13 species of *Myotis* in the United States and by many other bats, and this pattern must dominate their ecological strategies as well. The *Myotis* commonly having twins is the southeastern bat (*M. austroriparius*), which does not hibernate throughout southeastern winters and thus is subject to warm-weather mortality agents for most of the year (Rice, 1957). Restricted natality limits the adaptive flexibility of *M. lucifugus,* and in view of the recent influence of man this has become a detrimental specialization.

Little is known about the duration or importance of the commensal relation of little brown bats and humans. Owners of some nursery buildings in Indiana thought that their attics had been inhabited by bats for at least 70 to 80 years. A large number of the Indiana nurseries occupied houses of an architectural style popular from about 1850 to 1920. These were brick structures with wooden eaves and black slate roofs. Davis (1962) speculated that the aging of houses and clearing of forests have increased the amount of habitat suitable for *M. lucifugus* and that the species is more abundant now than before settlement of North America by Europeans. Fenton (1970) suggested that buildings might be more satisfactory places to rear young than natural structures and that extensive logging operations may have promoted development of the house-dwelling habit. We agree with these opinions.

We observed that as the standard of human living rose and people became more aware of the potential of bats for creating unpleasant odors and for carrying rabies and "bugs," more money was expended or effort made on extermination or major repair than would have been the case otherwise. New building materials and styles of architecture are less suitable for bat habitation, and deforestation and selective logging have eliminated most potential roost sites in trees. The effect of continued abandonment of farm buildings on nursery site availability is uncertain. We expect a decrease in availability of the preferred nursery microclimate in the study area and a corresponding decrease in the abundance of the little brown bat. We expect its density to decline below pre-settlement levels and do not foresee the establishment of management practices to halt that trend.

SUMMARY

1. This study was conducted in Indiana and north-central Kentucky from 1952 to 1969. Little brown bat populations in buildings and caves were periodically counted and sampled. A total of 71,706 bats was banded, and 10,760 individuals were recaptured a total of 14,336 times.

2. Female *M. lucifugus* spent the warm months in nursery populations, where they bore and reared their young. Nursery roosts were located in buildings and were typically hot, dark, and poorly ventilated. Most males spent the warm months in separate roosts, either individually or in small groups. *M. lucifugus* hibernated in caves during the winter. Air in winter roosts was cool, humid, and almost completely still.

3. Migration from nurseries to hibernacula was mostly from north to south. Distance of migration ranged from 10 to 455 kilometers.

Several other types of movement were associated with autumn migration. Bats dispersed from the nurseries in all directions. Some bats visited nurseries other than their natal sites during autumn dispersal. Bats arriving at the caves participated in an autumnal swarming behavior in which flight in and out of a cave occurred all night long. During this period few bats roosted in the cave in the daytime. Most individuals swarmed at a cave for only a few nights, but their subsequent autumn movements apparently did not include other caves. Bats usually used the swarming cave for winter hibernation and for swarming the following autumn, but a few moved elsewhere. *M. lucifugus* from Indiana nurseries concentrated their swarming activity at Indiana caves, whereas most of those swarming at the Kentucky caves were probably summer residents of Kentucky or extreme southern Indiana. Some swarming bats underwent a secondary dispersal, moving generally northward away from the caves to nurseries and other sites; females went farther than did males.

Most *M. lucifugus* spent each winter in the same cave, but changes of hibernaculum from one year to another were common.

In spring, *M. lucifugus* began "staging" activities, including cave-

to-cave movement and nocturnal flight similar to autumnal swarming behavior. Spring dispersal from the caves took the form of movement to the north, east, and west. Bats returned to the nurseries in spring migration.

In contrast to the substantial mixing of bats from different populations in autumn, winter, and spring, both sexes showed a high degree of nursery site attachment. Nursery populations were distinctly separate units. Movements from one nursery to another during summer were extremely rare, and females always spent each summer at the nurseries where they were born.

4. Arrival at nurseries began in mid-April and continued to the middle or end of May. Small declines in early June suggested departure of transient animals. Nursery population size virtually doubled when the young were born. Peak numbers of flying bats occurred in mid-July when all immatures were flying and migration had not begun. During autumn migration (or at least from late July through August), nursery population size fluctuated markedly, with several hundred bats leaving or arriving at a roost in one night. Distinct departure from nurseries began in early September and almost all bats were gone by early October.

5. Swarming activity at caves occurred at low or moderate levels from the third week of March to the first week of June. Low to high levels of activity were found from the last week of July to the third week of October. Numbers of *M. lucifugus* swarming in August and September varied considerably from one night to the next. Peaks and lows of activity occurred on the same night at two distant caves and activity appeared to follow similar phenological patterns from year to year.

6. Size of hibernating populations appeared to change markedly during winter. Large numbers of *M. lucifugus,* mostly females, must have spent portions of the winter undetected, either in parts of caves inaccessible to humans or at unknown sites.

7. The sex ratio of immatures was 1:1 shortly after birth and throughout the prevolant period. Among flying young, males apparently left the nurseries earlier than females.

Adults in nurseries were mostly females. Adult males were always scarce, but more were present in June and July than in the spring. A large southern nursery contained more males than

did northern nurseries; possibly most males remain relatively near the cave region in the summer.

Increased proportions of males in September and October resulted when males moved into the nurseries. This change was most prominent at a nursery near the caves.

8. Hibernating populations almost always consisted of more males than females. Sex ratios were closest to parity and most stable in mid-winter, and the highest proportions of males occurred in autumn and spring. Each cave or group of caves appeared to have its own characteristic mid-winter sex ratio. More northerly hibernacula tended to have higher proportions of males than southern caves.

9. Females bear young at the age of one year. Litter size is almost always one, and there is only one litter per year. The reproductive rate per female was 0.98 offspring per year. No variation in age-specific fertility is known or suspected in the study area.

10. Highest minimum survival rates were relatively low in the first year after banding but were much higher and apparently constant in subsequent years. Mean life expectancy of females was slightly more than two years. Maximum recorded longevity was 14 years.

Accidents while flying or seeking shelter constitute the major source of natural mortality. Natural mortality was negligible within nursery and winter roosts, except for rare cave flooding. Extermination or bat-proofing of nurseries resulted in loss of at least 52 per cent of the *M. lucifugus* in a decade. The decline as measured in winter populations appeared even more serious, perhaps as high as 80 per cent. Continued declines in abundance are expected.

11. Successful occupation of a niche with only seasonally available food depends on being energetically conservative and performing all species maintenance functions during the warm months. *M. lucifugus* must find roost sites with stable microclimates suitable for deep hibernation in winter and for both daily torpor of adults and rapid growth of immatures in summer.

12. Animals in the populations included in this study are members of a deme since they interbreed and are genetically isolated from individuals in outlying populations. Other studies

indicate that in eastern North America *M. lucifugus* occurs in relatively discrete demes. Swarming behavior brings together bats dispersed throughout the deme range to breed in a smaller area near the hibernacula. This behavior apparently prevents local inbreeding and increases the probability of finding mates.

13. Differences in summer-to-winter movement patterns are consistent with the view that these bats may migrate in groups and orient themselves by recognition of physiographic features.

14. Females regularly achieved their full biotic potential of one offspring each per year. As the average female produced one female offspring during her lifetime, undisturbed nursery populations appeared to be stable. Thus, populations would have had to greatly increase survival rates in order to grow.

LITERATURE CITED

Allen, A. A. 1921. Banding bats. J. Mamm., 2:53–57.

Allin, A. E. 1942. Bats hibernating in the district of Thunder Bay, Ontario. Canadian Field-Nat., 56:90–91.

Bailey, V. 1936. The mammals and life zones of Oregon. N. Amer. Fauna, 55:1–400.

Baker, R. J. 1964. *Myotis lucifugus lucifugus* (LeConte) and *Pipistrellus hesperus maximus* (Hatfield) in Knox County, new to north-central Texas. Southwestern Nat., 9:205.

Barbour, R. W., and W. H. Davis. 1969. Bats of America. Univ. Press Kentucky, Lexington, 286 pp.

Beer, J. R. 1955. Survival and movement of banded big brown bats. J. Mamm., 36:242–248.

Benton, A. H., and J. Scharoun. 1958. Notes on a breeding colony of *Myotis*. J. Mamm., 39:293–295.

Blatchley, W. S. 1896. Indiana caves and their fauna. Ann. Rept. Indiana Dept. Geol. Nat. Resources, 21:121–212.

Cagle, F. R., and L. Cockrum. 1943. Notes on a summer colony of *Myotis lucifugus lucifugus*. J. Mamm., 24:474–492.

Carmody, G. R., M. B. Fenton, and D. S. K. Lee. 1971. Variation of body weight and proteins in three Ontario populations of hibernating *Myotis lucifugus lucifugus* (LeConte) (Chiroptera: Vespertilionidae). Canadian J. Zool., 49:1535–1540.

Caughley, G. 1966. Mortality patterns in mammals. Ecology, 47:906–918.

Cockrum, E. L. 1969. Migration in the guano bat, *Tadarida brasiliensis*. Pp. 303–336, *in* Contributions in mammalogy (J. K. Jones, Jr., ed.), Misc. Publ. Mus. Nat. Hist., Univ. Kansas, 51:1–428.

———. 1970. Insecticides and guano bats. Ecology, 51:761–762.

Constantine, D. G. 1967. Activity patterns of the Mexican freetailed bat. Univ. New Mexico Publ. Biol., 7:1–79.

Cope, J. B., W. Baker, and J. Confer. 1961. Breeding colonies of four species of bats in Indiana. Proc. Indiana Acad. Sci., 70:262–266.

Cope, J. B., and D. R. Hendricks. 1970. Status of *Myotis lucifugus* in Indiana. Proc. Indiana Acad. Sci., 79:470–471.

Davis, R. 1966. Homing performance and homing ability in bats. Ecol. Monogr., 36:201–237.

Davis, W. H. 1962. Loss of our bat populations. Bat Res. News, 3:2–6.

———. 1963. Operation Chiroptera, 1963. Bat Res. News, 4:30–31.

———. 1967*a*. A *Myotis lucifugus* with two young. Bat Res. News, 8:3.

———. 1967*b*. Theoretical significance of tolerance to high temperatures by *Myotis lucifugus*. Bat Res. News, 8:13–14.

Davis, W. H., and H. B. Hitchcock. 1964. Notes on sex ratios of hibernating bats. J. Mamm., 45:475–476.

———. 1965. Biology and migration of the bat, *Myotis lucifugus*, in New England. J. Mamm., 46:296–313.

Davis, W. H., M. D. Hassell, and M. J. Harvey. 1965. Maternity colonies of the bat *Myotis l. lucifugus* in Kentucky. Amer. Midland Nat., 73:161–165.

DeBlase, A. F., S. R. Humphrey, and K. S. Drury. 1965. Cave flooding and mortality in bats in Wind Cave, Kentucky. J. Mamm., 46:96.

Deevey, E. S., Jr. 1947. Life tables for natural populations of animals. Quart. Rev. Biol., 22:283–314.

Dwyer, P. D. 1966. The population pattern of *Miniopterus schreibersii* (Chiroptera) in northeastern New South Wales. Australian J. Zool., 14:1073–1137.

———. 1969. Population ranges of *Miniopterus schreibersii* (Chiroptera) in south-eastern Australia. Australian J. Zool., 17:665–686.

Dymond, J. R. 1936. Life history notes and growth studies on the little brown bat, *Myotis lucifugus lucifugus*. Canadian Field-Nat., 50: 114–116.

Fenton, M. B. 1966. Parturition, growth, and milk dentition of the bat, *Myotis lucifugus lucifugus* (LeConte), in southeastern Ontario. M.S. thesis, Univ. Ontario, 52 pp.

———. 1969*a*. Ecological studies of bats in Ontario and adjacent regions. Ph.D. thesis, Univ. Toronto, 131 pp.

———. 1969*b*. Summer activity of *Myotis lucifugus* (Chiroptera: Vespertilionidae) at hibernacula in Ontario and Quebec. Canadian J. Zool., 47:597–602.

———. 1970. Population studies of *Myotis lucifugus* (Chiroptera: Vespertilionidae) in Ontario. Life Sci. Contrib., Royal Ontario Mus., 77:1–34.

Fitch, J. H. 1966. Weight loss and temperature response in three species of bats in Marshall County, Kansas. Search, 6:17–24.

Folk, G. E., Jr. 1940. Shift of population among hibernating bats. J. Mamm., 21:306–315.

Gates, W. H. 1936. Keeping bats in captivity. J. Mamm., 17:268–273.

Gifford, C. E., and D. R. Griffin. 1960. Notes on homing and migratory behavior of bats. Ecology, 41:378–381.

Glass, B. P., and C. M. Ward. 1959. Bats of the genus *Myotis* from Oklahoma. J. Mamm., 40:194–201.

Gould, E. 1955. The feeding efficiency of insectivorous bats. J. Mamm., 36:399–407.

Griffin, D. R. 1940*a*. Migration of New England bats. Bull. Mus. Comp. Zool., 86:216–246.

———. 1940*b*. Notes on the life histories of New England bats. J. Mamm., 21:181–187.

———. 1945. Travels of banded cave bats. J. Mamm., 26:15–23.

———. 1970. Migrations and homing of bats. Pp. 233–264, *in* Biology of bats (W. A. Wimsatt, ed.), Academic Press, New York, 1:xii + 1–406.

Griffin, D. R., and H. B. Hitchcock. 1965. Probable 24-year longevity records of *Myotis lucifugus*. J. Mamm., 46:332.

Guilday, J. E. 1948. Little brown bats copulating in winter. J. Mamm., 29:416–417.

———. 1950. Winter fetus in the little brown bat, *Myotis lucifugus*. J. Mamm., 31:96–97.

Guthrie, M. J. 1933*a*. Notes on the seasonal movements and habits of some cave bats. J. Mamm., 14:1–19.

———. 1933*b*. The reproductive cycles of some cave bats. J. Mamm., 14:199–216.

Guthrie, M. J., and K. R. Jeffers. 1938. Growth of follicles in the ovaries of the bat *Myotis lucifugus lucifugus*. Anat. Rec., 71:477–496.

Hahn, W. L. 1908. Some habits and sensory adaptations of cave-inhabiting bats. Biol. Bull., 15:135–193.

Hall, J. S. 1962. A life history and taxonomic study of the Indiana bat, *Myotis sodalis*. Sci. Publ. Reading Public Mus. and Art Gallery, 12:1–68.

Hall, J. S., R. J. Cloutier, and D. R. Griffin. 1957. Longevity records and notes on tooth wear of bats. J. Mamm., 38:407–409.

Hall, J. S., and N. Wilson. 1966. Seasonal populations and movements of the gray bat in the Kentucky area. Amer. Midland Nat., 75: 317–324.

Hall, J. S., and F. J. Brenner. 1968. Summer netting of bats at a cave in Pennsylvania. J. Mamm., 49:779–781.

Hammond, G. H. 1948. Mass migration of bats; Clarenceville, P. Q., 1931. Canadian Field-Nat., 62:124.

Heltsley, J. R. 1965. Bats and caves of the northwestern highland rim of Tennessee. M.S. thesis, Austin Peay State College, 114 pp.

Hitchcock, H. B. 1940. Keeping track of bats. Canadian Field-Nat., 54:55–56.

———. 1949. Hibernation of bats in southeastern Ontario and adjacent Quebec. Canadian Field-Nat., 63:47–59.

———. 1950. Sex ratios in hibernating bats. Bull. Nat. Speleol. Soc., 12:26–28.

———. 1965. Twenty-three years of bat-banding in Ontario and Quebec. Canadian Field-Nat., 79:4–14.

Humphrey, S. R. 1964. Extermination at Indiana *Myotis lucifugus* nurseries. Bat Res. News, 5:34.

———. 1971. Photographic estimation of population size in the Mexican free-tailed bat (*Tadarida brasiliensis*). Amer. Midland Nat., 86:220–223.

———. 1972. Adaptations of refuging freetailed bats. Bat Res. News, 13:19, 21–26.

Humphrey, S. R., and J. B. Cope. 1964. Movements of *Myotis lucifugus lucifugus* from a colony in Boone County, Indiana. Proc. Indiana Acad. Sci., 72:268–271.

Jones, J. K., Jr. 1964. Distribution and taxonomy of mammals of Nebraska. Univ. Kansas Publ., Mus. Nat. Hist., 16:1–356.

Krutzsch, P. H. 1961. A summer colony of male little brown bats. J. Mamm., 42:529–530.

Kunz, T. H. 1965. Notes on some Nebraskan bats. Trans. Kansas Acad. Sci., 68:201–203.

Layne, J. N. 1958. Notes on mammals in southern Illinois. Amer. Midland Nat., 60:219–254.

Licht, P., and P. Leitner. 1967. Behavioral responses to high temperatures in three species of California bats. J. Mamm., 48:52–61.

Lobeck, A. K. 1929. The geology and physiography of the Mammoth Cave National Park. Kentucky Geol. Surv., ser. 6, 31:327–399.

Lyman, C. P. 1970. Thermoregulation and metabolism in bats. Pp. 301–330, *in* Biology of bats (W. A. Wimsatt, ed.), Academic Press, New York, 1:xii + 1–406.

Lyon, M. W., Jr. 1925. Bats caught by burdocks. J. Mamm., 6:280.

Martin, R. L. 1961. Vole predation on bats in an Indiana cave. J. Mamm., 42:540–541.

MEARNS, E. A. 1898. A study of the vertebrate fauna of the Hudson Highlands, with observations on the Mollusca, Crustacea, Lepidoptera, and the flora of the region. Bull. Amer. Mus. Nat. Hist., 10:303–352.

MILLER, J. S. 1955. A study of the roosting habits, and of the environmental factors concurrent with the time of evening flight, of little brown bats (*Myotis lucifugus*) in Northern Lower Michigan. Ph.D. thesis. Univ. Michigan, 86 pp.

MILLER, R. E. 1939. The reproductive cycle in male bats of the species *Myotis lucifugus* and *Myotis grisescens*. J. Morph., 64:267–296.

MOHR, C. E. 1933. Observations on the young of cave-dwelling bats. J. Mamm., 14:49–53.

————. 1945. Sex ratios of bats in Pennsylvania. Proc. Pennsylvania Acad. Sci., 19:65–69.

MOISAN, G. 1961. *Myotis lucifugus* in Quebec winter sample. Bat Res. News, 2:16.

————. 1963. Cave samples of *Myotis lucifugus* in Quebec. Bat Res. News, 4:17.

MUIR, T. J., AND E. POLDER. 1960. Notes on hibernating bats in Dubuque County caves. Proc. Iowa Acad. Sci., 67:602–606.

MYERS, R. F. 1964. Ecology of three species of myotine bats in the Ozark Plateau. Ph.D. thesis, Univ. Missouri, 210 pp.

National Atlas of the United States. 1970. U. S. Geol. Surv., Washington, D. C., 417 pp.

PEARSON, E. W. 1962. Bats hibernating in silica mines in southern Illinois. J. Mamm., 43:27–33.

PHILLIPS, G. L. 1966. Ecology of the big brown bat (Chiroptera: Vespertilionidae) in northeastern Kansas. Amer. Midland Nat., 75:168–198.

RICE, D. W. 1957. Life history and ecology of *Myotis austroriparius* in Florida. J. Mamm., 38:15–32.

ROER, H. 1960. Vorlaufige Ergebnisse der Fledermaus-Beringung und Literaturubersicht. Bonner Zool. Beitr., 11:234–256.

RYSGAARD, G. N. 1942. A study of the cave bats of Minnesota with especial reference to the large brown bat, *Eptesicus fuscus fuscus* (Beauvois). Amer. Midland Nat., 28:245–267.

SCHNEIDER, A. F. 1966. Physiography. Pp. 40–56, *in* Natural features of Indiana (A. A. Lindsey, ed.), Indiana Acad. Sci., Indianapolis.

SHERMAN, A. R. 1929. Summer outings of bats during fourteen seasons. J. Mamm., 10:319–326.

SMITH, E. 1954. Studies of the life history of non-cave-dwelling bats in northeastern Ohio. Ohio J. Sci., 54:1–12.

————. 1957. Experimental studies of factors affecting sex ratios in the little brown bat. J. Mamm., 38:32–39.

SMITH, E., AND W. GOODPASTER. 1956. Adjacent roosts of *Eptesicus* and *Myotis*. J. Mamm., 37:441–442.

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. W. H. Freeman and Co., San Francisco, 776 pp.

STEGEMAN, L. C. 1954*a*. Variation in a colony of little brown bats. J. Mamm., 35:111–113.

————. 1954*b*. Notes on the development of the little brown bat *Myotis lucifugus lucifugus*. J. Mamm., 35:432–433.

STONES, R. C., AND T. OLDENBURG. 1968. Occurrence of torpid *Myotis lucifugus* in a cold mine in summer. J. Mamm., 49:123.

Stones, R. C., and J. E. Wiebers. 1965. A review of temperature regulation in bats (Chiroptera). Amer. Midland Nat., 74:155–167.

Studier, E. H., and M. J. O'Farrell. 1972. Biology of *Myotis thysanodes* and *M. lucifugus* (Chiroptera: Vespertilionidae)—I. Thermoregulation. Comp. Biochem. Physiol. 41A:567–595.

Tinkle, D. W., and I. G. Patterson. 1965. A study of hibernating populations of *Myotis velifer* in northwestern Texas. J. Mamm., 46:612–633.

Walley, H. D. 1971. Movements of *Myotis lucifugus lucifugus* from a colony in LaSalle County, Illinois. Trans. Illinois Acad. Sci., 63:409–414.

Wimsatt, W. A. 1944*a*. Further studies on the survival of spermatozoa in the female reproductive tract of the bat. Anat. Rec., 88:193–204.

———. 1944*b*. An analysis of implantation in the bat, *Myotis lucifugus lucifugus*. Amer. J. Anat., 74:355–411.

———. 1945. Notes on breeding behavior, pregnancy, and parturition in some vespertilionid bats of the eastern United States. J. Mamm., 26:23–33.

Zimmerman, F. R. 1937. Migration of little brown bats. J. Mamm., 18:363.

INDEX

Adaptive flexibility, 70
Age at first flight, 40

Deme, 62–67
Dispersal, see movement, site attachment
Distribution, 1, 3, 4, 6, 61–64
Disturbance, 20–21, 55–60

Eptesicus fuscus, 3, 30, 60

Flight behavior, 5
Food supply, 61, 62

Habitat availability, 70
Hibernation, 6, 61

Lasiurus cinereus, 54
Limiting factors, 62, 69–70

Methods:
  age determination, 2, 27, 28, 29
  counts, 2, 18–22
  estimates, 18, 24–25, 56, 59
  samples, 2
Microclimate, 3–5, 6, 61–62, 70
Migration, see movement
Mortality, human-related, 55–60
  in hibernacula, 58–60
  in nurseries, 55–58
Mortality, natural, 14, 53–55
  in flight or migration, 14, 53–55
  in hibernacula, 54–55
  in nurseries, 53–54
Mortality rates, see survival
Movement:
  dispersal, autumn, 7–9, 27
  dispersal, secondary autumn, 13–14
  dispersal, spring, 15
  group, 20, 67–68
  migration, autumn, 7–8, 20, 68
  migration routes, 68
  migration, secondary autumn, 14
  migration, spring, 15, 19–20, 32–33
  regional patterns of, 11–13, 62–68
  spring staging, 15, 25, 32–33, 35–36
  summer, 15
  swarming, 9–11, 30, 32–33, 65–66
  transient nursery visitation, 7–9, 19–20, 29–30
  wandering, 64–65
  winter, 14–15
Myotis:
  keenii, 26
  lucifugus carissima, 3, 66
  lucifugus lucifugus, 2, 64
  lucifugus occultus, 3, 66
  sodalis, 24, 59

Natality, see reproduction

Pesticides, 57, 60
Population:
  declines, 55–60, 69–70
  growth, 69
  size, 18–26, 55–56, 58–59, 69–70
  structure, 21–22, 27–37
Populations:
  nursery, 3–5, 18–22, 27–30
  shelter, 5–6, 30–32
  swarming, 22–24, 32–33, 65–66
  winter, 6, 24–26, 33–37
Predation, 54–55

Recaptures, 2, 7–17, 43–55, 57–58, 62–65, 66–67

Reproduction:
age at sexual maturity, 38
biotic potential, 68–69
copulation, 38–39, 66
litter size, 40–41
maternal care, 40
natality rate, 40–42, 68–70
ovulation, 39
parturition, 39–40
Roost structure:
buildings, 3–6, 25–26, 70
caves, 5–6, 25–26
trees, 3, 4, 26, 70

Seasons, defintion of, 2
Site attachment, 11, 14–17, 62, 69
Survival:
annual survival rates, 53, 69
first year after marking, 48
life tables, 44–45, 48–49, 51–52
maximum longevity, 53
mean life expectancy, 53, 69
method of data analysis, 43, 47–48
survival curves, 46–47, 50

Temperature, see microclimate
Thermoregulation, 3–5, 61–62

Vespertilio subulatus, 26

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